Designing Tropical Forests of the Future to Mitigate Climate Change and Safeguard Biodiversity

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By

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I, Charlotte Elizabeth Wheeler confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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Abstract

The restoration of degraded tropical lands can lead to carbon sequestration, which can mitigate climate change, alongside safeguarding biodiversity and providing other co-benefits. Recently tropical counties have pledged to restore millions of hectares of degraded lands to forest. However, important gaps in policy-facing knowledge remain. To address these I firstly assessed the rate that naturally regenerating forests sequester carbon, by systematically reviewing studies measuring forest recovery following the abandonment of agricultural lands. I found a mean aboveground carbon sequestration rate of 2.5 Mg C ha^{-1} yr^{-1} (± 0.6, 95% CI) over 100 years, which was not dependent on prior land use (*n*=71 studies).

Next, I measured the results of active restoration of tropical forest, via fire exclusion and planting native seedlings, on abandoned agricultural land in Kibale National Park, Uganda. Aboveground carbon sequestration was 1.9 Mg C ha^{-1} yr^{-1} (± 0.4; *n*=50 x 0.05 ha permanent sample plots) and tree species richness (≥10 cm diameter at breast height) increased from 0 to 5 species per plot in the first 18 years after restoration (1995-2013).

I then measured the results of active restoration of tropical forest via planting native seedlings and climber cutting, in selectively logged forest in Sabah, Borneo. Restored forest sequestered aboveground carbon twice as fast as selectively logged control forest (3.3±0.9 and 1.6±0.8 Mg C ha^{-1} yr^{-1}, respectively; 24 x 0.2 ha plots, half restored, half controls) over eight years (2007-2015), and had higher tree species richness (48 and 35 species ≥10 cm DBH per plot, respectively).

Lastly, I estimate the impact of fulfilling the global aspiration of restoring 350 million ha of tropical lands to forest by combining restoration pledges (including the proportion of land committed to native forest and forms of tree-based agriculture), with sequestration rates. Implimentation would remove 0.4 Pg C yr^{-1} from the atmophere over the next 100 years. Restoration is therefore shown to offer climate-relevant sequestration potential, and if active restoration is used then these future forests can be designed to optimise multiple benefits to humanity.

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List of Abbreviations

AGB	Aboveground biomass
AGC	Aboveground carbon
AGWP	Aboveground wood production
AIC	Akaike information criterion
Al	Aluminium
ANOCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
BA	Basal Area
BGB	Belowground biomass
BGC	Belowground carbon
C	Carbon
Ca	Calcium
CBD	Convention on Biological Diversity
CO_2	Carbon Dioxide
CUE	Carbon Use Efficiency
DBH	Diameter at Brest Height
DVCA	Danum Valley Conservation Area
eCEC	Effective Cation Exchange Capacity
ENSO	El Niño–Southern Oscillation
FAO	Food and Agricultural Organisation
FLR	Forest Landscape Restoration
GHG	Greenhouse Gas
GPP	Gross Primary Productivity
H	Height
ha	Hectare
INFAPRO	Innoprise-FACE the Future Rainforest Rehabilitation Project
IPCC	Intergovernmental Panel on Climate Change
ITTO	The International Tropical Timber Organization
IUCN	International Union for Conservation of Nature
K	Potassium
LAI	Leaf Area Index
LiDAR	Light Detection and Ranging
MAP	Mean Annual Precipitation
MASL	Meters Above Sea Level
MAT	Mean Annual Temperature
Mg	Magnesium
Mg	Megagram
Mt	Megaton
N	Nitrogen
N_2O	Nitrous Oxide

Na	Sodium
NMDS	Non-metric Multidimensional Scaling
NPP	Net Primary Productivity
NTFP	Non-Timber Forest Products
P	Phosphorous
PC	Principal Component
PCA	Principal Components Analysis
Pg	Petagram
POM	Point of Measurement
PPM	Parts per Million
PPTQ	Precipitation in the driest quarter
PSP	Permanent sample plot
REDD+	Reducing Emissions from Deforestation and forest Degradation
Tg	Teragram
UNEP	United Nations Environmental Programme
UNFCCC	United Nations Framework Convention on Climate Change
UWA-FACE	Uganda Wildlife Authority - FACE the Future Forest Restoration Project
WD	Wood density
WRI	World Resource Institute
yr	Year
YSFMA	Yayasan Sabah Forestry Management Area

1. Introduction

1.1. Project rational

Reducing emissions from deforestation and forest degradation and increasing the carbon content per unit area within the worlds forests, via restoration, reforestation and afforestation, are all strategies to mitigate the effect of climate change, and have been receiving increasing international attention over the past few years (Bellassen and Luyssaert, 2014, Canadell and Raupach, 2008, Houghton et al., 2015). This is mainly because approximately 12% of global CO_2 emissions come from deforestation and forest degradation, second only to the burning of fossil fuels (IPCC, 2013). In the past, mitigation efforts have focused on the reduction of deforestation and forest degradation to avoid the release of CO_2. However, more recently the importance of enhancing carbon storage on degraded and abandoned tropical lands via forest restoration has been noted (Chazdon, 2008). It is suggested that this could happen through carbon offsetting schemes, such as Reducing Emissions from Deforestation and forest Degradation (REDD+), which aims to offer financial incentives to developing countries in return for reducing carbon emissions (Bullock et al., 2011, Angelsen, 2008). Additionally many countries view the multiple benefits forest provide as important and provide incentives to expand forest cover.

Tropical forests are considered to have particularly high potential for carbon sequestration as they have high above ground biomass (AGB) per unit area and therefore high carbon density estimated at approximately 100 Mg C ha^{-1} (Baccini et al., 2012, Saatchi et al., 2011, FAO, 2011), compared to 58 Mg C ha^{-1} and 40 Mg C ha^{-1} in Temperate and boreal forests, respectively (Thurner et al., 2014). Tropical forests have higher above ground net primary productivity (NPP), of between 12 and 15 Mg C ha^{-1} yr^{-1} (del Aguila-Pasquel et al., 2014, Kho et al., 2013, Malhi, 2012), compared to temperate and boreal forest estimated at between 6 to 9 Mg C ha^{-1} yr^{-1} and 4 to 5 Mg C ha^{-1} yr^{-1} respectively (Malhi et al., 1999, Luyssaert et al., 2007). Tropical forest also offer temperature reductions that are up to three times greater than those observed in temperate and boreal forests, (Arora and Montenegro, 2011). This is because, forest which appear darker than

open land, especially where snow is lying, such as in boreal and northern temperate forests, reduces surface albedo, exerting positive radiative forcing effects. The positive forcing effects of afforestation in high latitude regions could outweigh the negative forcing effects of carbon sequestration, thereby causing a net increase in temperature (Betts, 2000).

Furthermore, there are large areas of degraded land available in the tropics, estimated at around 850 million ha (ITTO, 2002), that could be restored to increase carbon storage. Areas of deforested and degraded tropical land are often abandoned for a number of reasons. For example, in areas cleared for agricultural crop production, depletion of soil nutrients over successive growing seasons can lead to reductions in crop yield, forcing cultivators to move on to new areas (Benayas et al., 2007). In the case of selectively logged forest, areas are abandoned immediately to allow the forest to recover, until timber species grow to a merchantable size and an area can be re-logged. Repeated logging eventually leads to diminished returns (Putz et al., 2012), therefore logging efforts are moved elsewhere and the remaining severely degraded forest is abandoned.

Such areas of abandoned land are able to naturally regenerate (Poorter et al., 2016), following the processes of secondary succession, eventually resembling old growth forest if given a sufficient amount of time (Guariguata and Ostertag, 2001). Estimates suggest that naturally regenerating tropical lands currently sequester approximately 1.6 Pg C yr^{-1} globally (Pan et al., 2011, Grace et al., 2014). However, natural regeneration on abandoned land can often be very slow or halted altogether in severely degraded lands in a process termed arrested succession. A number of different factors can lead to arrested succession the most common of which is fire. Degraded tropical forests are particularly susceptible to fire (Cochrane, 2003), and fire can lead to a positive feedback mechanism, whereby areas that have been burnt once are liable to repeated burnings (Cochrane et al., 1999). Poor seed dispersal in highly fragmented landscapes (Cubiña and Aide, 2001), and a limited soil seed and seedling bank (Guariguata and Ostertag, 2001) in abandoned land can limit regeneration of native seedlings. Soils in abandoned land can also be severely degraded, cultivation can deplete soils of nutrients (Uhl et al., 1982), reducing nutrient availability for seedlings, and heavy machinery used for logging can lead to soil compaction increasing soil penetration resistance (Hattori et al., 2013). Finally, the spread of invasive species in abandoned land can also lead to arrested succession. Disturbed areas are more susceptible to invasion by fast growing native and exotic species (Lonsdale, 1999) due to increased

resource availability in the form of light, alongside climate conditions, which are more favourable to heliotropic, invasive species as opposed to native forest specialist species (Van Kleunen et al., 2010). The combination of these factors acting simultaneously, can limit natural regeneration in abandoned land. Therefore active management interventions to restore tropical forest ecosystems may be necessary overcome arrested succession.

Active forest restoration can involve a number of different management strategies to overcome the problems associated with arrested succession including: fire management or the use of silvicultural techniques, such as the slashing of invasive grasses and shrubs or planting of native species (Lamb, 2010, Chazdon, 2008). Such management interventions aim to accelerate the rate of natural regeneration thereby enhancing carbon sequestration above levels seen in naturally regenerating forest, whilst simultaneously improving ecosystem services and offering biodiversity co-benefits (Venter et al., 2012).

Well-planned and large-scale restoration in specific areas offers the greatest benefits for carbon sequestration and biodiversity (Chazdon and Uriarte, 2016). The larger the area restored the greater the carbon benefits, and strategic placement of restoration efforts could help make tropical forests more resilient to climate change. For example, creating buffer zones around forest fragments, in vulnerable drought prone regions, could help reduce the risk of fires. Furthermore, undertaking restoration between forest fragments could help increase habitat connectivity, allowing for the dispersal of species across the landscape. This will be particularly important in helping species respond to climate change by shifting their ranges (Proctor et al., 2011).

It is likely that different types of degraded tropical land will have different recovery trajectories under natural regeneration, and that the rate of recovery can be modified following active ecological restoration. It is also probable that more severely degraded land would require more intensive management. However, there is currently very little understanding about how active ecological restoration affects the rate of carbon sequestration and biodiversity recovery, in areas that have undergone different types of degradation.

Furthermore, whilst undertaking active forest restoration, or allowing abandoned lands to naturally regenerate, could offer large carbon and biodiversity benefits (e.g. Gilroy et al., 2014), when conducting forest restoration at a landscape scale, it is unlikely that

restoration back to an intact forest state would take place over an entire landscape. A more likely scenario is that multiple land uses would be integrated within the landscape (IUCN and WRI, 2014). This may include areas of actively restored or naturally regenerating forest, alongside other tree bases agricultural systems such as agroforestry and timber plantations, which could offer other benefits such as food and timber production (Chazdon et al., 2015). However, the carbon storage potential of landscape scale restoration, which incorporates different land use types is poorly quantified. Currently there are international commitments to restore 350 million ha of forest globally by 2030 (UNFCCC, 2014), therefore, improving knowledge of carbon storage from landscape scale restoration is essential to understand the climate change mitigation potential of restoration at such a large scale.

This highlights two large gaps in research that this project aims to answer. Firstly, what is the rate of forest recovery, in terms of carbon sequestration and increased floral diversity, in areas that have undergone different types of land use change, and how can active ecological restoration modify this recovery rate? Secondly, over large areas realistically how much carbon can be sequestered in restored tropical forests?

1.2. Tropical forests

1.2.1. Tropical forest definition and extent

Put simply, tropical forests are tree-dominated ecosystems found within the tropics of Cancer and Capricorn (N 23.5^0 to S 23.5^0). However, beyond this it is difficult to reach a unanimous definition, as tropical forest habitats do not exist as a stand-alone entity, but instead exist along ecological gradients, transitioning from closed canopy forest to woody savannah systems (Lewis, 2006, Torello-Raventos et al., 2013). The United Nations Food and Agricultural Organization (FAO) defines forest as land with tree cover over 10%, with trees that reach >5 m height at maturity, covering an areas of more than 0.5ha (FAO, 2000). However, this definition covers a vast array of forest types, each with a habitat specific forest structure and carbon density including; moist lowland tropical forest (AGB, Phillips et al., 2008), high altitude montane forest (Moser et al., 2011), open woodland forest such as the Miombo woodlands of east Africa (Shirima et al., 2011), and coastal mangrove forests (Donato et al., 2011). Despite the broad array of forest types, in general terms tropical forests tend to be characterized by high rainfall, relatively low to moderate soil fertility, high temperature, high biodiversity and high above ground biomass and carbon storage. Within the context of this research I define tropical forest as closed canopy forest (>30% canopy cover, Archard et al., 2014, Saatchi et al., 2011), located within the tropics and open canopy forests (<30% canopy cover, Archard et al., 2014, Saatchi et al., 2011) are defined as woodland.

The extent and carbon content of tropical forest has been well studied, however, there is still a great deal of variability in estimates at both a regional and global scale (E.g. Achard et al., 2002, Achard et al., 2004, Eva et al., 2012, Mayaux et al., 2005, Stibig et al., 2014). Differences in estimates are dependent on different methodologies used and the working definition used for 'forest'. This means direct comparison between estimates of forest area can be difficult. However, there is a general consensus that globally forests cover approximately 40 million km^2, approximately 50% of which is in the tropics (FAO, 2010).

From the most recent research, I estimate an average of 23.2 million km^2 of tropical forest, with canopy cover over 10%, remaining between 2007 and 2010 (Table 1), with a mean carbon density of 100 Mg C ha^{-1} (Table 2). Southeast Asian forests have the highest carbon

density at 117 Mg C ha^{-1}, and African forests have the lowest at 80 Mg C ha^{-1}, with Latin American forests being intermediate between the two other continents at 110 Mg C ha^{-1} (Table 2, No data is available for Australia). Total pan-tropical above ground carbon storage is approximately 319 Pg C (Table 3). Geographically in descending order, 52% (166 Pg C) of tropical forest carbon is stored in Latin America, 29% (94 Pg C) in Africa, 18% (56 Pg C) in Southeast Asia, and 2% (7 Pg C) in Australia (Table 3).

Table 1. Estimates of tropical forest extent by continent and total area in km^2.

	Total forest extent (>10% Canopy cover)					Woodland extent (10 - 30% Canopy cover)		
	Pan (2011)	Achard (2014)	FAO (2011)	Saatchi (2011)	Mean	Achard (2014)	Saatchi (2011)	Mean
Year of estimate	2007	2010	2010	ND		2010	ND	
Africa	6.8 (35)	11.6 (47)	6.0 (31)	7.8 (32)	8.1 (35)	6.8 (70)	3.3 (42)	5.0 (58)
Americas	9.7 (50)	9.1 (37)	8.9 (46)	12.1 (49)	9.9 (43)	1.7 (17)	3.2 (41)	2.4 (28)
Southeast Asia	3.0 (15)	4.2 (17)	2.9 (15)	4.7 (19)	3.7 (16)	1.3 (13)	1.4 (18)	1.4 (15)
Australia	ND	ND	1.5 (8)	ND	1.5 (6)	ND	ND	ND
Total area (Million km^2)	19.5	24.9	19.3	24.6	23.2	9.8	7.8	8.8

Area reported from Achard (2014) are for forested land with tree cover >30% and forested land + other wooded land defined as tree cover >5 m tall and >10% tree cover still fitting in with the FAO definition of forest as used in other studies. The year of estimate is shown, ND = No data available. Percentage of total forest area per continent shown in parenthesis.

Of the studies estimating tropical forest cover, Achard et al. (2014) estimate the extent of tropical woodland, splitting land cover into forest with canopy cover >30 % and woodland with a canopy cover between 10% and 30%. Saatchi et al. (2011) also estimated carbon content in areas with canopy cover of between 10 and 30%. An average of 8.8 million km^2 of woodland area remain in 2010 (Table 1). However, these studies differ in the geographical distribution of woodland; Achard et al. (2014) estimated that 70% of woodland is found in Africa, whilst Saatchi et al. (2011) estimated that the cover of woodland is approximately the same in Southeast Asia and Latin America with just over 40% each (Table 1). These differences in estimates likely reflect the different methodological approaches use for estimating land cover, with Achard et al. (2014) using Landsat imagery at a 30 m resolution and Saatchi et al. (2011) using LiDAR imagery as a 1 km resolution. Estimates of tropical carbon storage also contain large uncertainties, with

over 200 Pg C difference between the smallest estimate by FAO (2011) and the largest estimate by Saatchi et al. (2011) (Table 3). These large differences in estimates of total carbon storage are due to differences in methodology and spatial extent of individual studies. For example, estimates from Saatchi et al. (2011) cover a much larger area than those from Baccini et al., (2012) leading to much higher estimates of total tropical carbon storage. The more recent study by Avitabile et al. (2016) integrates data from both the Saatchi et al. and Baccini et al. studies, and therefore is likely to present more accurate estimate of total carbon storage.

Table 2. Mean tropical forest carbon density (Mg C ha^{-1}) by continent and pan-tropically.

	Saatchi (2011)	Baccini (2012)	FAO (2011)	Mean
Africa	80	82	79	80.3
Americas	99	116	115	110.0
Southeast Asia	137	119	95	117.0
Australia	ND	ND	ND	ND
Global	100	106	95	100.3

ND = No data available.

Table 3. Total tropical forest carbon storage (Pg C) by continent and pan-tropically.

	Avitabile (2016)	Saatchi (2011)	Pan (2011)	Baccini (2012)	FAO (2011)	Mean
Africa	96	113	79.2	129	52.1	93.9 (29)
Americas	186	193	139.8	216	95.5	166.1 (52)
Southeast Asia	92	107	43.2	18	27.5	57.5 (18)
Australia	ND	ND	ND	ND	6.6	6.6 (2)
Global	374	413	262.2	363	181.7	318.8

Percentage of total C shown in parentheses, ND = No data available.

1.2.2. Environmental conditions

1.2.2.1.Climate

Mean annual temperature (MAT) and mean annual precipitation (MAP) is high across tropical forests, with a pan-tropical MAT of 25.4 ˚C and MAP of 2180 mm yr^{-1}, with MAP in some regions reaching >6000 mm yr^{-1} at the highest end of the scale (Hijmans *et al.,* 2005,Table 4). Cross-continental differences in MAT are minimal, differing by just 1.4 ˚C, with the lowest MAT in Australia and the highest in Latin America (Table 4). Cross-continental differences in MAP are much greater, with Asian tropical forests receiving the highest rainfall at 2840 mm yr^{-1} and the lowest seen in African tropical forest at 1650 mm yr^{-1} (Malhi and Wright, 2004,Table 4.).

Table 4. Regional and pan-tropical mean annual precipitation (MAP, mm), mean annual temperature (MAT, ˚C) and dry season length (months).

	MAP (mm)	MAT (˚C)	Dry season length (months)
Latin America	2358 (314)	25.6 (0.8)	3.2 (1.5)
Africa	1651 (95)	24.8 (0.9)	4.5 (0.8)
Southeast Asia	2839 (361)	25.4 (0.1)	2.1 (1.2)
Australia	1700 (ND)	24.2 (ND)	7.0 (ND)
Pan-tropical mean	2178 (488)	25.4 (0.9)	3.7 (1.8)

Adapted from data in Malhi and Wright (2004). Standard deviation in parenthesis, ND = No data available.

The intra-annual variability of MAT is generally low, with most tropical forest regions maintaining a relatively constant temperature throughout the year. However, tropical forests experience a great deal of seasonality in rainfall distribution, with some regions having prolonged dry seasons of up to seven months (Table 4). Distance from the equator is an important determinant in tropical forest seasonality, with forests further away from the equator generally having higher intra-annual variability and therefore higher water stress (Malhi and Wright, 2004). Such changes in rainfall seasonality are able to impact forest function. Evapotranspiration in a fully wetted tropical forest is estimated to be approximately 100 mm $month^{-1}$ (Malhi et al., 2002). During periods when evapotranspiration exceeds rainfall tropical forest may become water stressed, experiencing a net water deficit, which in turn can limit photosynthesis. Water limitations

on photosynthesis, during the dry season can reduce AGB production, and it is thought that the rate of AGB production depends on the amount of precipitation received throughout the dry season (Malhi et al., 2006). However, dry season length, dry season intensity and temperature also influence water stress and must be considered to fully understand the impact of rainfall on tropical forests

Evidence from the Amazon basin and Southeast Asia suggests that AGB and wood productivity correlates with both MAP and dry season length. A study by Malhi et al. (2006) found a decrease in basal area and AGB, with increasing water stress, in areas that experienced a prolonged dry season (> four months). Another study from the Amazon by Saatchi et al. (2007) found that AGB density decreased as dry season length increased. And similarly, in Southeast on the island of Borneo, Slik et al. (2010) found that AGB and basal area both increased with increasing rainfall, and decreasing seasonality.

Tropical forests can also experience large inter-annual variability in both rainfall and temperature that can greatly affect forest structure; this variability is closely related to the El Niño southern oscillation (ENSO). El Niño events occur when there is a combined shift in sea-surface temperature and atmospheric pressure in the Pacific Ocean, which occurs on a three to seven year cycle (Malhi and Wright, 2004). Southeast Asia typically has high rainfall brought in by the Pacific ocean, during an El Niño event this effect shifts rainfall to the central Pacific ocean, leading to extreme drought in some regions, particularly in; Australia, Indonesia and New Guinea (Banin, 2010). These events can lead to major changes in forest cover and structure; for example the El Niño of 1997-1998 led to extreme drought conditions and subsequent forest fires in Indonesia. In Kalimantan alone this resulted in the loss of approximately 3 million ha of tropical forest (Fuller et al., 2004), and across Indonesia an estimated 0.2 to 2.6 Pg C were released into the atmosphere through the burning of forests and the underlying peat (Page et al., 2002).

1.2.2.2.Soils

The distribution and formation of soils is determined by a number of factors including; topography, climate, parent material and age (Jenny, 1941), leading to a great deal of heterogeneity in soil type at both local and continental scales. Tropical forest soils are predominantly highly weathered, with moderate to low fertility, due to the hot and humid conditions that promote nutrient leaching and soil erosion (Quesada *et al.*, 2010,Table 5).

Soils can determine the structure and function of tropical forests, with soil fertility leading to changes in AGB, wood density and productivity (Quesada et al., 2012, Ter Steege et al., 2006).

Table 5. Description of the commonest tropical soil types and location.

Soil type (WRB)	Soil type (USDA)	Description	Location	Fertility
Ferralsols	Oxisols	Deeply weathered, low pH, deep and physically stable, low chemical fertility, low cation retention	Continental shields of South America & Africa (Amazon & Congo Basins)	Low
Alisols	Ultisols	Low base saturation, unstable so susceptible to erosion, high Al concentration	Latin America, West Africa, East African highlands, Southeast Asia	Low
Acrisols	Ultisols	Strongly weathered, low pH, low base saturation	Southeast Asia, Southern fringes of Amazon basin	Low
Nitosols	Ultisols	Deep, well drained, permitting deep rooting making soil resistant to erosion, one of the most productive tropical soils	African highlands (>1000 m), Latin America and Southeast Asia	Moderate - High

Soil types based on the world reference base for soil (WRB) and U.S. Department of Agriculture (USDA) soil classification systems. (IUSS working group WRB, 2014)

For example, a pair of studies by Quesada et al. (2010) and Quesada et al. (2012) showed the Amazon basin has a strong west to east gradient in soil fertility and forest structure. They found high fertility, shallow soils in Western Amazonia, which was correlated with higher stem turnover rates and wood production, alongside low wood density, suggesting that trees have a "live fast, die young" strategy in this region, resulting in lower AGB. Conversely in Eastern Amazonia soils were deeper and had low fertility, which was coupled with slower wood production and stem turnover, and trees with a higher wood density, leading to higher AGB. They suggested that the steep topography of the Western Amazon, lying along the Andean foothills, together with shallow soils, has allowed for weathering of the underlying parent material, which continually replenishes depleted nutrients. Meanwhile, the gentle topography and continuous deep weathering in the Eastern Amazon over millennia has effectively eliminated bedrock as a source of nutrients,

leading to lower fertility soil in this region. Similar trends in changes to AGB and wood density related to soil fertility have also been observed by Laurance et al. (1999), Mitchard et al. (2014) and Ter Steege et al. (2006) in the Amazon.

However, in Southeast Asia and Africa different relationships between soil fertility and forest structure have been observed. A study by Lewis et al. (2013) across Africa and another by Slik et al. (2010) in Borneo both found that AGB was positively correlated with soil fertility, the opposite of what was observed in the Amazon. Additionally Lewis found that high AGB was related to clay rich soils, suggesting that well structured soils are needed to support very large trees that store the majority of AGB.

Studies such as these demonstrate how changes in soil properties can alter forest structure; however, the relationship between soil properties and AGB does not seem to be consistent across the tropics. High soil fertility in the Amazon is linked to higher wood production but lower AGB, whereas in Africa and Southeast Asia high soil fertility is related to high AGB. However, soil properties are not the only factor determining AGB and wood production, the combination of both edaphic and climatic conditions are important in determining forest structure and function.

1.2.2.3.Biodiversity

Tropical forests are the most diverse terrestrial ecosystem on earth (Gibson et al., 2011) containing approximately 60% of all species globally (Dirzo and Raven, 2003). Recent estimates by Mora et al. (2011) and Scheffers et al. (2012) estimate that across the globe there are 8.7 and 8.4 million species, respectively, with species defined as a multicellular organism. The consistency of these predictions suggests that these estimates are more accurate than historical estimates of global species richness, which have ranged from 1.5 up to 100 million species (Dirzo and Raven, 2003, May, 2000).

Not only are tropical forests very diverse, they also harbour a large number of endemic species. Indeed, 15 of the 25 biodiversity hotspots put forward in the seminal paper by Myers et al. (2000) are located within the tropics. Biodiversity hotspots are defined as areas that contain at least 1500 of the globes 300,000 endemic plants and have lost at least 70% of their original cover. Within these 15 tropical hotspots Myers estimated there were

70% of the 300,000 endemic plant species and 78% of the 27,300 endemic vertebrate species, demonstrating the high level of endemism within tropical forest.

Tropical tree diversity is high at between 50 and 300 species ≥10 cm DBH per ha^{-1} (Ter Steege et al., 2003, Gentry, 1988, Whitmore, 1984, Valencia et al., 1994) and an estimated 53,000 species across the tropics (Slik et al., 2015). Slik et al. (2015) estimated that approximately 24,000 species are found in both Latin American and Southeast Asian forests, whereas Africa is much more depauperate with just 6000 species. However, the diversity of tree species has been estimated to make up just 15 to 20% of plant diversity in tropical forest, with epiphytes, herbs and shrubs contributing 56-61% of plant species (Gentry and Dodson, 1987). The distribution of tree diversity is not uniform across large spatial scales. For example, across the Amazon basin, the peak of tree diversity is in the Northwestern corner, in Peru and central Amazonia. With the northern and southern fringes of the Amazon having the lowest tree diversity (Ter Steege et al., 2003).

Faunal diversity is also exceptionally high, particularly that of invertebrates, with an estimate 2.5 to 3.7 million invertebrates species across the tropics is more accurate (Hamilton et al., 2010). This high invertebrate diversity is a vital component of tropical forests as invertebrates perform a number of essential functioning roles such as pollination, decomposition, herbivory of invasive plant species, predation of invertebrate pests and nutrient cycling (Lavelle et al., 2006, Wilson, 1987). Alongside invertebrates, there is also a high diversity of vertebrate species in tropical forests (Jenkins et al., 2013). These species are also important as it is estimated that 94% of flowering plants are pollinated by vertebrates and invertebrates in the tropics (Ollerton et al., 2011). The higher plant diversity and high proportion of invertebrate pollinated plants is also thought to lead to the high degree of host specificity observed in the tropics (Novotny and Basset, 2005), where a single or very limited number of species are able to pollinate a particular plant species. It is evident that a highly diverse flora and fauna community is distinctive of tropical forest, and that this is essential within tropical forests to maintain normal ecosystem function as different species perform innumerable functional roles within the forest.

1.2.3. Tropical forest structure

The combined factors of high precipitation, high biodiversity, high temperature and the soil conditions present, help determine the unique structure of tropical forest. The dominant life form, in terms of biomass, in tropical forests is trees. Trees are typically tall with high wood density, growing in high densities, contributing to a large basal area. The combination of these factors means tropical forests attain high AGB and therefore high carbon density. However, the structure of tropical forest is not uniform across the globe.

On average, South American forests have a high stem density (≥10 cm DBH) coupled with a mean wood density of 0.61 g cm^3, however their relatively short stature (35.8 m, Table 6) means they have the lowest AGB, of 318.3 Mg ha^{-1}, in comparison to other tropical continents (Table 6). However, across the Amazon average tree height varies with trees ≥40 cm DBH being significantly taller in the Guyana shield (Northeast Amazon), at 35.2 m, than in the other areas, where average tree height is <30 m (Feldpausch et al., 2011). This corresponds with a strong Southwest to Northeast gradient across the Amazon basin, of increasing wood density and decreasing soil fertility (Ter Steege et al., 2006, Quesada et al., 2012), which had led to higher AGB being observed in Northeast Amazon (Mitchard et al., 2014, Malhi et al., 2006).

Southeast Asian forests have a similar stem density and wood density to South American forest (Table 6). However, basal area is over 6 m^2 ha^{-1} higher in Asian forests, and asymptotic height is 58.3 m, around 13 m and 22 m taller than African and South American forest respectively (Table 6). This gives Southeast Asian forest the highest AGB of all the topical regions. However, unlike Africa and South America who have the majority of their forest in a single contiguous area in the Congo and Amazon basins, Southeast Asian forest are split over the mainland and many smaller islands.

Meanwhile, African forests are characterized low stem density, high wood density and intermediate height trees, compared to the other tropical forest continents. This gives African forest an AGB intermediate between South America and Southeast Asia, at 396 Mg ha^{-1} (Table 6). It has been suggested that this low stem density coupled with high wood density could demonstrate relatively low disturbance in African forest, allowing trees to attain greater size and self-thin (Lewis et al., 2013). A theory supported by the widespread occurrence of monodominant forests in Africa. Monodominant forests are tropical forest dominated by a single species (E.g. *Gilbertiodendron dewevrei* or *Cynometra alexandri*), and

are thought to occur over areas that have experienced limited disturbance in the recent past (Peh et al., 2011).

Table 6. Cross-continental comparison of forest structure and AGB from forest plot networks in intact moist tropical forest.

	Africa	Asia	South America
Stem density (≥10 cm DBH ha^{-1})	425.6 (11.1) [a]	591.2 (37.0) [b]	592.0 (14.0) [c]
Wood Density (g cm^3)	0.65 (0.01) [a]	0.60 (0.02) [b]	0.61 (0.01) [d]
Basal Area (m^2 ha^{-1})	30.3 (0.8) [a]	36.5 (1.7) [b]	30.0 (1.1) [d]
Median tree height (10-20 cm DBH)	14.0 [e]	15.7 [e]	14.1 [e]
Median tree height (20-40 cm DBH)	22.3 [e]	25.1 [e]	23.8 [e]
Median tree height (≥40 cm DBH)	33.5 [e]	34.7 [e]	28.2 [e]
Asymptotic height (m)	45.1 (2.6) [f]	58.3 (7.5) [f]	35.8 (6.0) [f]
GPP (Mg C ha^{-1} yr^{-1})	30.8 (5.3) [g]	31.2 [h]	27.9 (3.4) [h]
NPP (Mg C ha^{-1} yr^{-1})	13.9 (1.7) [g]	12.8 [h]	9.7 (1.6) [h]
CUE (NPP/GPP)	0.45 [g]	0.41 [h]	0.4 (0.04) [h]
AGB (Mg ha^{-1})	395.7 (14.3) [a]	458.2 (27.1) [b]	318.3 (11.7) [d]

All AGB estimates calculated using the moist tropical forest equation including tree height from Chave et al. (2005). Values in parentheses are 95% CI where available, where missing no data is available. *a* = Lewis et al. (2013), *b* = Slik et al. (2010), *c* = Lewis et al. (2004b), *d* = Baker et al. (2004b), *e* = Feldpausch et al. (2011), *f* = Banin et al. (2012), *g* = Fisher et al. (2013), *h* = Malhi (2012). In Asia data from *b* are specifically from Borneo, whereas data from *e* and *f* are from across Southeast Asia.

1.2.4. Tropical forest function

Tropical forests play an important part of the global carbon cycle. Different processes working in unison determine the baseline dynamics of tropical forest carbon cycle; beginning with, the assimilation of CO_2 via photosynthesis, termed gross primary productivity (GPP). GPP is the largest annual flux within the global carbon cycle, estimated at 120 Pg C yr^{-1} (Beer et al., 2010). Some of this carbon is released into the atmosphere via autotrophic (plant) respiration (R_a), from different plant organs. The remaining carbon is used to form plant structural organs, termed net primary productivity (NPP). Carbon is then transferred to the soil via decomposition and transport from root networks. Finally, carbon is released back into the atmosphere via heterotrophic (microbial) respiration (R_h) completing the cycle (Malhi and Grace, 2000, Grace, 2004).

There have been some attempts to quantify the internal carbon cycle of tropical forest. For example, del Aguila-Pasquel et al. (2014) measured the carbon dynamics of an aseasonal forest in Northwest Amazon, Peru which experienced little water stress. They estimate GPP to be approximately 39.1 Mg C ha^{-1} yr^{-1} (Figure 1), of which 24.9 Mg C ha^{-1} yr^{-1} is released back into the atmosphere via R_a and the remaining 14.1 Mg C ha^{-1} yr^{-1} is used to form plant structures (NPP, Figure 1). Once carbon is eventually transferred to the soil, 18.1 Mg C ha^{-1} yr^{-1} is released via R_h. The fraction of NPP to GPP is termed the carbon use efficiency (CUE) and describes the fraction of fixed carbon allocated to producing new tissue, estimated by del Aguila-Pasquel et al. (2014) at 0.36 (Figure 1). However variation in carbon dynamics has been observed. Malhi et al. (1999) conducted a similar study near Manaus, Brazil, in an area that experiences a 4 month dry season. They found a similar NPP (15.6 Mg C ha^{-1} yr^{-1}) to that of del Aguila-Pasquel et al. (2014), however, GPP, R_a and R_h were all approximately 9 Mg C ha^{-1} lower, at 30.4 Mg C ha^{-1} yr^{-1}, 14.8 Mg C ha^{-1} yr^{-1} and 9.7 Mg C ha^{-1} yr^{-1} respectively, producing a higher CUE of 0.51. It is possible that the differences in abiotic conditions at these two sites could result in different carbon dynamics.

Unfortunately few similar studies have been conducted in tropical Asia and Africa. A review by Malhi (2012) found ten studies reporting one of GPP, NPP or CUE across the tropics. Of these studies, seven were conducted in South America, three in Asia and none in Africa. They found that on average Southeast Asian forests had slightly higher GPP and NPP in comparison to South American forests but they both had similar CUE (Table 6). A study by Fisher et al. (2013) estimated GPP and NPP for African forest using land surface models as opposed to ground based methods, predicting a GPP of 30.8 Mg C ha^{-1} yr^{-1} and an NPP of 13.9 Mg C ha^{-1} yr^{-1}, giving a CUE of 0.45 (Table 6).

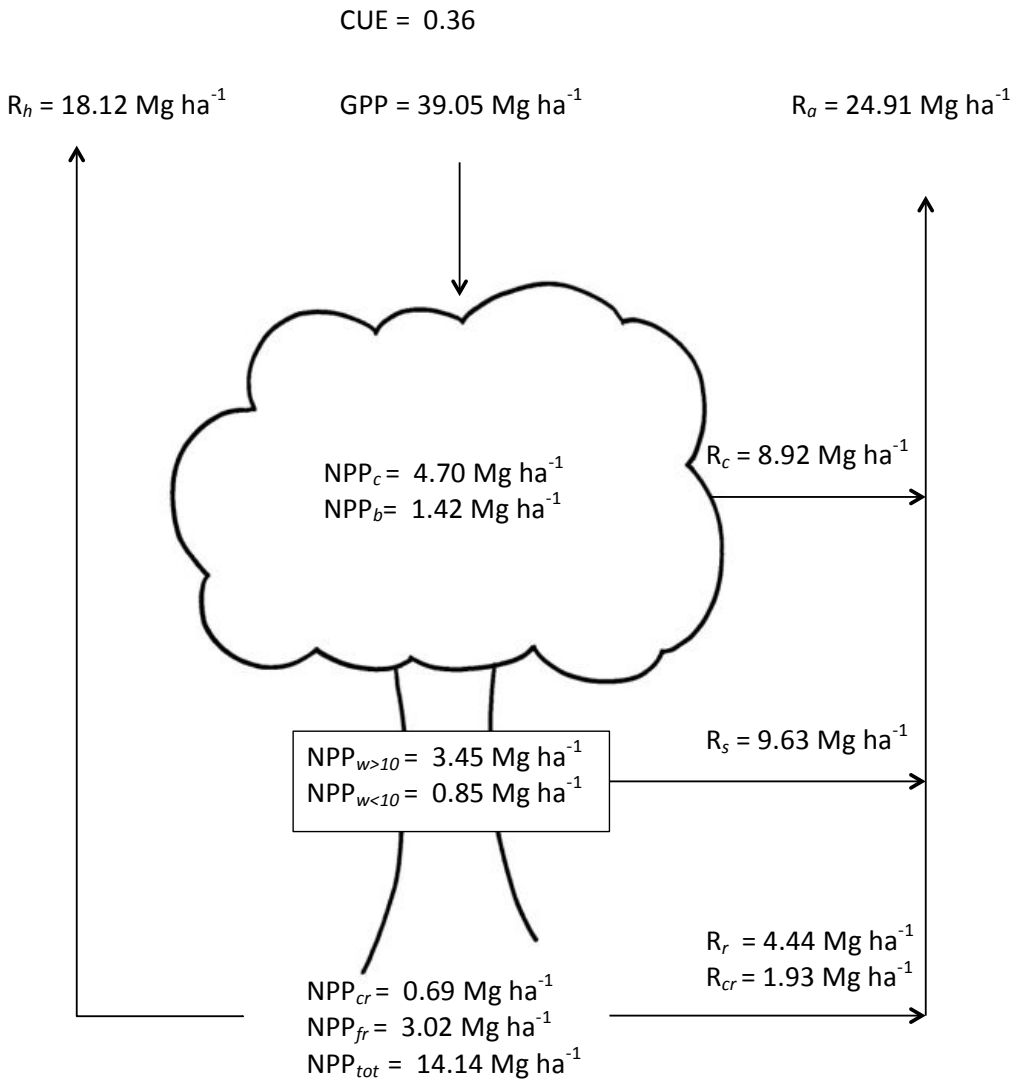

Figure 1 Tropical forest carbon fluxes. Showing gross primary productivity (GPP), total net primary productivity (NPP_{tot}), autotrophic respiration (R_a), heterotrophic respiration and carbon use efficiency (CUE). NPP_{tot} is the sum of canopy (NPP_c), branch (NPP_b), woody stems <10 cm DBH ($NPP_{w<10}$), woody stems >10 cm DBH($NPP_{w>10}$), coarse roots (NPP_{cr}) and fine roots (NPP_{fr}) net primary productivity. R_a is the sum of canopy respiration (R_c), stem respiration (R_s), rhizosphere respiration (R_r) and coarse root respiration (R_{cr}). All values in Mg C ha^{-1} yr^{-1} except CUE, which is the ratio of NPP: GPP. Adapted from figure in del Aguila-Pasquel et al. (2014).

Forests assimilate carbon into cellulose, starch and proteins via photosynthesis. These compounds are used to produce organic plant structures including; woody tissue, root tissue, leaf tissue and volatile organic compounds (Malhi et al., 2011), together these structures form the biomass found in a forest. The rate of biomass accumulation, and

therefore carbon sequestration, is determined by NPP. The allocation of NPP for different plant structures helps determine ecosystem function within a forest; NPP used for woody tissue is predominantly related to carbon storage. The allocation of NPP to leaf tissue determines fruit and flower production, total leaf area and the photosynthetic capability of an ecosystem, and finally the allocation of NPP to fine roots can determine the rate of water and nutrient uptake (Malhi et al., 2011). It has been estimated that NPP is allocated approximately equally between woody tissue, leaf tissue and fine root tissues in tropical forests (Malhi et al., 2011) allowing for the different processes involved in biomass accumulation to occur.

The tropical forest carbon cycle is not only dependent on the assimilation of carbon into plant biomass but also the residency time of carbon within plant structures and soil before returning to the atmosphere (Galbraith et al., 2013, Malhi et al., 1999). In particular the residency time of carbon within woody structures is important, as these are the most carbon dense plant structure. Galbraith et al. (2013) estimated a pan-tropical mean woody biomass residency time of 51 years (n = 177 plots), with South America having the shortest residency time at 47 years,, followed by Asia (59 years) and then Africa (65 years). There is evidence that suggests changes in forest dynamics, such as changes to stem turnover rates, could affect residence time. Increases in tropical forest stem turnover rates have been observed since the 1950's in the Amazon (Phillips and Gentry, 1994), which has generally been attributed to increased CO_2 concentrations (Lewis et al., 2004a). It is likely that there is a trade-off between tree growth rates and longevity, with higher growth rates, as a result of CO_2 fertilisation, causing increased mortality (Galbraith et al., 2013). Increased tree mortality in effect causes a decrease in woody biomass residency time, therefore, diminishing the sink ability of forests. However the same study by Galbraith et al. (2013) noted that this effect could be counteracted by stimulation of NPP.

Overall the carbon balance of tropical forests is very complex and is determined by both NPP and carbon residency time. An understanding of both these processes is important to determine the long-term carbon balance of tropical forests. However, detailed data about these processes is not well understood pan-tropically, particularly in Africa, where there is a need for further research.

1.3. Tropical forest ecosystem services

Tropical forests are important not only for their intrinsic value, but also for the numerous ecosystem services they provide, including; watershed protection, soil protection, climate regulation, carbon sequestration and biodiversity protection, all of which are critical for sustained ecosystem function and human wellbeing. Furthermore, tropical forests provide numerous resources including timber and non-timber forest products, which sustain the livelihood of millions of people globally. However, when tropical forest habitats undergo disturbance, ecosystem services are diminished. The more heavily disturbed and ecosystem is the greater the impact on the ecosystem services provided by that habitat. The importance of natural ecosystems for human wellbeing is well documented, and is now more widely understood thanks to reports such as the Millennium Ecosystem Assessment (MEA, 2005). Within the framework of the Millennium Ecosystem Assessment the types of services ecosystems are divided into four categories; provisioning, regulating, cultural and supporting services (MEA, 2005, See Figure 2 for description of services). Here the ecosystem regulating and provisioning services specifically provided by tropical forests are reviewed, and the effect of disturbance on these services is described.

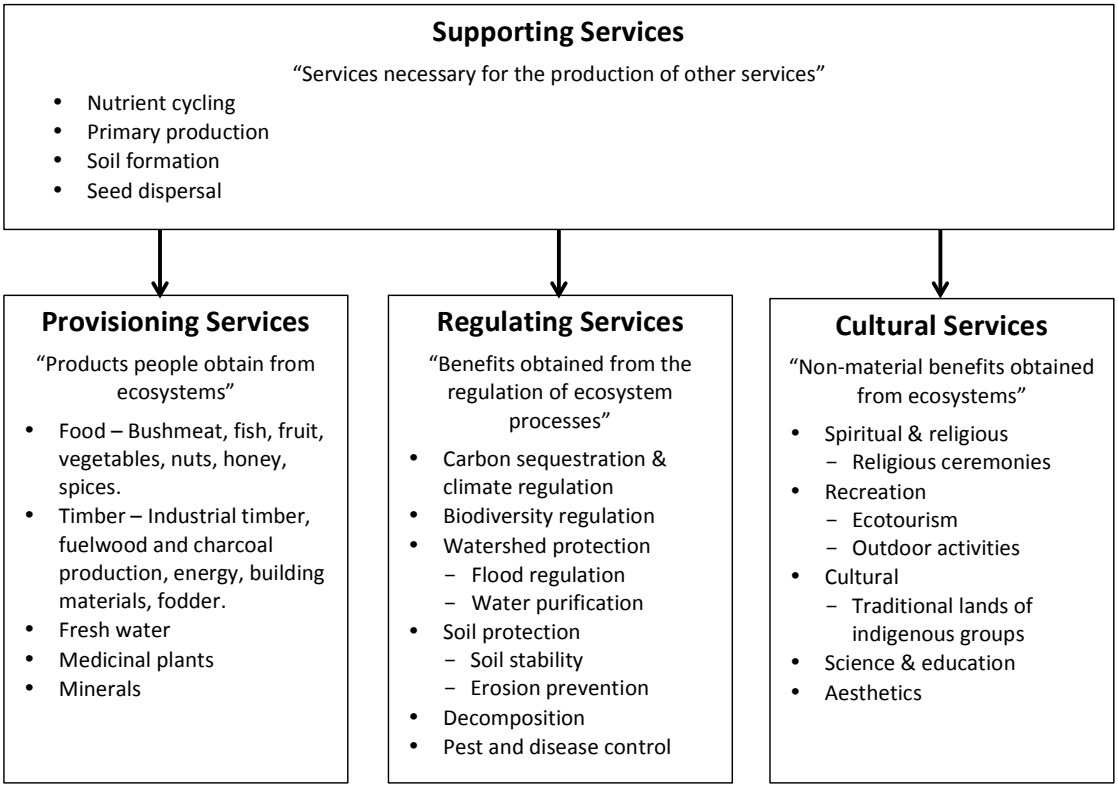

Figure 2. Overview of the four types of ecosystem services and examples of these services. Adapted from MEA (2005) figure 1.1.

1.3.1. Regulating services

1.3.1.1.Climate regulation

Tropical forest ecosystems are able to influence climate at a local to global scale. This is due to two processes; the absorption of solar radiation which is related to the surface albedo of forests, and the rate of evaporation into the atmosphere (Meir et al., 2006). Tropical forests receive high solar radiation, compared to temperate regions, estimated at 13.7 MJ m^2 d^{-1} (MJ = Megajoules, Banin, 2010), the fraction of this radiation that is reflected back to the atmosphere (surface albedo), can influence temperature, as it affects how much solar radiation is absorbed by the land surface (Meir et al., 2006). Forests appear dark, absorbing more radiation than non-forested land creating a general warming effect (Meir et al., 2006, MEA, 2005). The opposing cooling effect of evaporation also occurs in tropical forests, with root structures taking in water for photosynthesis and releasing it back into the atmosphere via transpiration. A second effect that increases

evaporation is also present in tropical forest, whereby, the complex vegetation present increases surface roughness which in turn increases wind turbulence around the surface, increasing evaporation (Meir et al., 2006). This cooling effect of evaporation in tropical forests releases large quantities of water vapour into the atmosphere creating cloud cover and subsequent rainfall. Meaning that the presence of tropical forest itself is important for creating the high rainfall it receives, and therefore changes to forest cover can impact climate at a local scale.

1.3.1.2. Carbon storage and sequestration

Closely linked to the climate regulation services, is carbon sequestration and storage of tropical forest. Tropical forests are an important component of the global carbon cycle, storing 318 Pg C (Table 3) and cycling large quantities of carbon via photosynthesis and respiration (Beer et al., 2010). The ability of tropical forest to be a net source or net sink of carbon is dependent on the balance of three large carbon fluxes: carbon sequestration by intact forest, carbon sequestration by regrowth forest and emissions from deforestation and forest degradation (Pan et al., 2011, Grace et al., 2014). Current estimates suggest that tropical forests are currently a small source of approximately 0.1 Pg C yr^{-1} when all three fluxes are considered together (Pan et al., 2011). However, without the carbon sequestration in intact and regrowth forest, tropical forests would be a much larger carbon source to the atmosphere.

There is an increasing body of evidence suggesting that old-growth tropical forests are acting as a carbon sink. Studies using permanent sample plots monitoring long-term changes in AGB have been conducted in Africa and the Amazon. A study by Lewis et al. (2009) in African forests estimated a carbon sink of 0.63 Mg C ha^{-1} yr^{-1} between 1968 and 2007. Extrapolated across all African forests this produces a total carbon sink of 0.34 Pg C yr^{-1}. This effect has also been observed in Amazonia, two studies conducted by Baker et al. (2004a) and Phillips et al. (2008) estimated an Amazonian carbon sink of 0.62 Mg C ha^{-1} yr^{-1}, similar is size to that observed in Africa. Across the whole of the Amazon this equated to a total carbon sink of 0.79 Pg C yr^{-1}. This suggests that increasing carbon storage in intact old-growth tropical forest is a pan-tropical phenomena, with a total carbon sink estimated to be 1.3 Pg C yr^{-1} across all tropical forests (Lewis et al., 2009). This intact

forest sink has generally been attributed to a CO_2 fertilization effect, which contributes to higher rate of photosynthesis and subsequent higher rates of NPP (Lewis et al., 2009).

However, Brienen et al. (2015) recently found that there has been a long-term decline in the Amazon forest sink of approximately 30%, from 0.54 Pg C yr^{-1} in the 1990's to 0.38 Pg C yr^{-1} in the 2000's. This decline is due to increases in mortality being twice as large as increases in productivity. These changes in forest function could be a result of two intense droughts in the Amazon in 2005 and 2010 (Marengo et al., 2011), which have already been shown to cause reductions in the carbon sink capacity of the Amazon (Phillips et al., 2009b) Phillips et al. (2009b) estimated that prior to the 2005 drought there was a carbon sink of 0.42 Mg C ha^{-1} yr^{-1}. However, immediately following the 2005 drought the rate of carbon sequestration dropped to -0.33 Mg C ha^{-1} yr^{-1}, demonstrating the sensitivity of tropical forest to drought, which is worrying considering the occurrence of drought is predicted to increase as the effects of climate change increase (IPCC, 2013, Malhi et al., 2008). However, while this evidence suggests there is currently a carbon sink in intact tropical forests it is possible that this effect could saturate at high CO_2 concentrations. Therefore intact tropical forest should not only be viewed as just a carbon sink but more importantly as a huge carbon store in their intact state.

1.3.1.3.Biodiversity protection

Tropical forests are important not only as a repository of biodiversity, but also for the ecosystem services that biodiverse habitats provide. More biodiverse ecosystems are considered to be more resilient to perturbations in local climate, have increased stability, are more resilient to disease and pests and have higher productivity (Cardinale et al., 2011, Hooper et al., 2005).

The numerous ecosystem services provided by tropical forests, including nutrient cycling, maintenance of soil structure and plant pollination, require a wide variety of species being present. More diverse habitats are able to support and sustain such services and have been shown to be more resilient to disturbances. Having a diverse mix of species that fill different niches and are sensitive to different fluctuations in environmental conditions means that ecosystems are more resilient to change and are therefore more stable

(Hooper et al., 2005). Temporal fluctuations in environmental conditions lead to slight changes in species composition, with some species become locally more abundant undertaking the functional roles left by other species (Ives and Carpenter, 2007). By having a number of different species performing similar functional roles, if one particular species becomes locally extinct as a result of disturbance there are number of different species that are able to fill that gap, allowing the ecosystem as a whole continues to function as normal (Hooper et al., 2005). This effect depends on slightly asynchronous responses of different species that perform a particular function with some species doing better than others due to a) the slightly different niche that each species fills resulting in different responses to disturbance and b) competitive release whereby the removal of one species performing a particular functional role, leaves way for another species to perform that same role (Hooper et al., 2005). When these effects are averaged out over time it leads to an overall more stable ecosystem (Doak et al., 1998).

More diverse ecosystems have also been shown usually to be more productive. This is often attributed to one of two theories, either sampling effects or complementarity. Sampling effects theory suggests that a few key species are particularly efficient at performing particular functional roles within an ecosystem; therefore higher diversity increases the likelihood of a key species being present (Schwartz et al., 2000). Whilst complementarity theory suggests more diverse ecosystems have reduced interspecific competition due to niche differentiation (Hooper et al., 2005). Meaning that different species use slightly different resources at slightly different times, thereby allowing for complete utilization of resources, which are converted to biomass (Cardinale et al., 2012). Species in monoculture plantations generally flower in synchrony and require the same resources, therefore do not utilize all available resources, compared to a group of species with different resource requirements (Cardinale et al., 2012). It is likely that these two opposing theories are not mutually exclusive, but instead sit at either end of a continuum from pure dominance to pure complementarity, with actual ecosystem responses lying somewhere in the middle as suggested by Loreau et al. (2001).

In low diversity systems the influence of biodiversity on productivity is clear. For example, A meta-analysis of 59 different studies by Cardinale et al. (2011) measured differences in productivity between monoculture and mixed species plantations. They found that the most diverse plantations had on average 1.43 times higher biomass than monocultures.

However, the importance of this effect in 'hyper-diverse' tropical forest is less clear. A study by Ruiz-Jaen and Potvin (2010) assessed the influence of tree diversity, environment (slope and soil properties) and spatial heterogeneity on AGC, reasoning that the latter two factors could mask the effects of diversity on productivity. Together these three factors accounted for 44% of the variation observed in AGC. With, tree diversity explaining the largest amount of variation (20%), suggesting there may be a link between AGC and diversity, alongside other environmental and spatial factors.

However, the relationship between biodiversity and productivity is possibly dependent on spatial scale. Chisholm et al. (2013) assessed the biodiversity and productivity relationship at three spatial scales (0.04ha, 0.25 ha and 1ha plots). At the smallest spatial scale, productivity and AGB were positively related to biodiversity, with a doubling of species richness leading to an increase in productivity by 48% and increase in AGB by 53%. However at larger spatial scales the relationship was neutral or negative, they concluded that over small spatial scales sampling effects and complementarity were important, but at large spatial scales environmental gradients drive productivity. Another similar study by Hubbell (2006) using spatial scales of 0.025ha, 0.25ha and 1ha, found no relationship between basal area (used as a proxy for AGB) and diversity even at the smallest spatial scale. These opposing results demonstrate the uncertainty in the relationship between biodiversity and productivity, particularly in diverse tropical forests.

The shape of the relationship between biodiversity and ecosystem function, which is generally asymptotic in shape (Cardinale et al., 2011), could possibly explain these results. Increasing numbers of species does not lead to a continual increase in productivity, there is a saturation effect at which point the addition of more species does not improve ecosystem function further (Cardinale et al., 2012). As biodiversity increases initially there is a rapid increases in ecosystem function, but this response gradually levels off as ecosystems become more diverse such as found in old-growth forests (Cardinale et al., 2012, Hooper et al., 2005). This effect also works in the opposite direction, with losses of a small number of species causing little change to ecosystem function, but as loss of diversity increases the loss of ecosystem function is accelerated eventually leading to a collapse in ecosystem function (Hooper et al., 2005).

1.3.1.4. Watershed protection

The watershed protection services that forest provide are highly important, with over 75% of the global population being served by water runoff from forests (MEA, 2005). Approximately 35% of rainfall in tropical forests is intercepted by the canopy (Bruijnzeel, 2004), and is either used in transpiration or evaporates off the leaf surface back into the atmosphere. Water that is not used in photosynthesis or intercepted by the canopy makes its way to streams, with water gradually filtering through the soil into water channels (Bruijnzeel, 1990). Under natural conditions old-growth tropical forest, with their extensive rooting systems, helps provide a slow release of water into streams (Bruijnzeel, 2004). Meanwhile, limited soil compaction within forest also means there is greater infiltration of water into soils, therefore water does not remain as surface runoff (Martínez and Zinck, 2004). The combination of these effects means that intact forest can help minimize the effects of flooding during the rainy season.

1.3.1.5. Soil protection

Tropical forests help protect soils in three main ways. Firstly, the presence of extensive root systems found in tropical forest increases soil stability. This is particularly important in steep hilly areas, as the removal of forests from steep hillsides has been shown to increase the risk of landslides (Mugagga et al., 2012). Unstable soil lead to soil erosion, therefore natural forest cover can help limit erosion into watercourses (Ehigiator and Anyata, 2011).

Secondly, forest cover with extensive root networks helps maintain soil structure, with soil compaction in natural forest much lower than in disturbed forests. This allows for rapid infiltration of water into soil (Bruijnzeel, 2004) and allows for the growth of seedlings, as the increased bulk density of compacted soils increases soil penetration resistance, which can lead to stunted growth of seedlings (Hattori et al., 2013).

Finally, forests are important for nutrient cycling in soils. The increased soil stability and decreased soil compaction in tropical forests both help reduce erosion of nutrient rich

topsoil soil (Lal, 2005), which ultimately helps retain soil nutrients. However forest cover also helps replenish nutrients through the decomposition of leaf litter and coarse woody debris (Vitousek and Sanford, 1986).

1.3.2. Provisioning services

1.3.2.1. Timber

The selective logging of timber occurs across the globe over vast areas, with an estimated 11 million ha yr^{-1} harvested (MEA, 2005). The International Tropical Timber Organisation (ITTO) estimated that a total of 173.6 Million m^3 of timber were extracted in 2012 alone, valued at over $2.5 billon (ITTO, 2012). However, there is huge regional variation in the rate of timber extraction with 60% (104 million m^3) of tropical timber coming from Asia, 23% from Latin America (40 million m^3) and 16% from Africa (29 million m^3). Indeed Indonesia, the worlds biggest producer of timber, provided 26% (46 million m^3) of the global total in 2012, more timber than either Africa or Latin America (ITTO, 2012). However, these estimates do not account for illegal logging meaning that actual extraction rates are higher. Quantifying illegal logging is difficult, however, is purported to be 20% of legally extracted timber (MEA, 2005).

These figures show the importance of timber extraction for the economies of many tropical countries. However, whilst the extraction of timber is an important provisioning ecosystem service, it inevitably leads to the simultaneous deterioration of other ecosystem services provided by undisturbed tropical forests. In particular regulating ecosystem services such as biodiversity protection and soil protection. Therefore, to maintain timber extraction as an ecosystem service and to reduce the detrimental effects of timber extraction on other ecosystem services, sustainable harvest of timber is necessary, such as using reduced impact logging techniques (Martin et al., 2015)

Tropical forests also provide fuelwood, either for direct use or charcoal production. Between 2000 to 2005, an estimated 1090 to 1240 Million m^3 yr^{-1} of fuelwood were extracted (MEA, 2005, FAO, 2010), meaning that fuelwood extraction accounts for over 75% of all timber extraction in the tropics. In 2004, 560 million households relied on

fuelwood and charcoal for energy, corresponding to 2.7 billion people, and such high levels of use are predicted to continue until 2030 (Maes and Verbist, 2012). This high consumption reflects the importance of fuelwood for the energy needs of people in developing countries, providing up to 70% of household energy (MEA, 2005, Mead, 2005).

1.3.2.2.Non-timber forest products

Non-timber forest products (NTFP) are goods of biological origin other than wood, derived from forests (FAO, 1999), including products such as food, animal fodder, construction materials, and medicinal plants among others. NTFPs are vital for the livelihoods of millions of people in the tropics, with 200 to 300 million people being reliant of NTFP to support their way of life (MEA, 2005).

NTFPs are important in two main ways; firstly, for direct consumption and secondly by creating income. Direct consumption includes the consumption of food products and fodder crops to feed livestock (Shackleton and Pandey, 2014). The direct consumption of NTFP represents a direct saving of money that would otherwise have to be spent on these items. For example, Saha and Sundriyal (2012) estimated the value of NTFPs in Arunachal Pradesh state, India, to be \$275 yr^{-1} per household. This is a large saving for many poor rural communities that often subsist of very low incomes of less than \$1 per day (Shackleton and Pandey, 2014) .

Income generation through the sale of NTFPs is also very important for millions of people. It has been estimated that the sale of NTFPs contributes between 5% and 90% of total household income in the tropics (Shackleton and Pandey, 2014). Whilst a large proportion of income generation is on a local subsistence level with products being sold at local markets, there is also national and international market for NTFPs mainly in the form of food products, medicinal plants and bamboo. For example, the international trade in edible NTFPs is estimated to be \$2.5 billion per year (MEA, 2005), showing the importance of NTFPs not only for local income generation but also the economies of developing countries.

One NTFP of particular importance to human wellbeing is medicinal plants and the use of medicinal plants for the development of pharmaceuticals. In a study by Saha and Sundriyal

(2012) they found that 50% of the 340+ species of plants commonly extracted from forest, were used for medicinal purposes. Many medicinal plants are used to extract and develop chemical compounds used in modern medicines including drugs for heart disease, cancer and HIV. Already up to 90% of drugs prescribed in the USA contain a compound that was originally derived from forest plants (MEA, 2005). A study by Mendelsohn and Balick (1995), used the total number of discovered drugs derived from tropical plant species and the total number of plant species in the tropics, to estimate the number of undiscovered drugs that could be derived from tropical plants. They estimated that there were at least another 375 drugs that could be derived from tropical forest plants, which would be of significant importance to global health.

1.3.3. Summary of ecosystem services

The combination of all of these ecosystem services together makes tropical forests in their natural state extremely important. Maintenance of these services allows for normal ecosystem function. The direct economic benefits of tropical forest provisioning service are clear, as they provide timber, fuel, food and medicinal plants. However direct benefits to humans of regulating services may be less obvious. A study by Costanza et al. (1998) estimated the value of ecosystem services at a global scale. The estimated the total value of ecosystem services to be \$33 trillion yr^{-1}, of which \$3.8 trillion yr^{-1} came from the tropics. They estimated the four most valuable tropical ecosystem services to be; nutrient cycling, raw materials, erosion control and climate regulation, which combined provided \$1700 ha^{-1} yr^{-1}. Which shows the economic importance that ecosystem services provide to humanity. However tropical forest cover is being lost rapidly and with that comes degradation of ecosystem services, which results in direct impacts on ecosystem function (MEA, 2005).

1.4. Land use change in the tropics: deforestation and forest degradation

1.4.1. Rate of deforestation and forest degradation

Estimates of deforestation rates vary, however, there is an overall consensus that deforestation is slowing, from 13.3 million ha yr^{-1} between 1990 and 2000 to 11.3 million ha yr^{-1} between 2000 and 2010 (Table 7). Geographically, Southeast Asia has the slowest absolute deforestation rate at 2.5 million ha yr^{-1} between 2000 and 2010 (Table 7). Latin America has the highest absolute deforestation rate at 5.0 million ha yr^{-1} between 2000 and 2010, with Africa being intermediate between the other two continents (Table 7). However, proportionally Southeast Asia has the highest deforestation due to lower total forest extent (Table 1), loosing 0.68% of the total forest area per year, between 2000 and 2010, compared to 0.51% in Latin America and 0.47% in Africa. All studies estimate Latin America has the highest deforestation rate, with the exception of FAO (2011), which estimated that Africa has the highest deforestation rate (Table 7).

Table 7. Rate of deforestation in millions ha yr^{-1} by region and pan-tropically for the periods 1990 – 2000 and 2000 – 2010.

		Africa	Americas	Southeast Asia	Global
1990-2000	Pan (2011)	4.4	5.6	3.5	13.5
	Achard (2014)	4.0	5.8	2.9	12.7
	FAO (2011)	6.6	4.6	2.6	13.7
	Mean (95% CI)	5.0 (1.6)	5.3 (0.7)	3.0 (0.5)	13.3 (0.6)
2000-2010	Pan (2011)	4.3	4.8	3.0	12.1
	Achard (2014)	3.4	6.0	2.8	12.1
	FAO (2011)	5.9	4.2	1.6	11.8
	Hansen (2013)	1.5	4.8	2.8	9.1
	Mean (95% CI)	3.8 (1.8)	5.0 (0.7)	2.5 (0.6)	11.3 (1.4)

The extent of degraded forest; defined as reduction in stocking volume within a forest leading to a reduction in AGB and ecosystem services including; biodiversity, soil protection and watershed protection (FAO, 2000), is more uncertain. As forest degradation is caused by a reduction in forest AGB rather than a change in land-use from 'forest' to 'non-forest', it is far more difficult to quantify using conventional optical remote sensing instruments (Putz and Redford, 2010, DeFries et al., 2007). However, new technologies such as radar and spaceborne LiDAR are helping to overcome these difficulties in mapping forest degradation (E.g. Mitchard et al., 2012).

Despite these problems there have been some attempts to estimate the extent of degraded forest. The FAO estimated a total of 9 million km^2 (Africa = 5.2 million km^2; South America = 2 million km^2; Southeast Asia = 1.8 million km^2) of secondary regrowth forest (FAO, 2010), defined as any forest not classed as primary forest or plantation forest and therefore covers a large spectrum of degraded, abandoned and regrowth forest following various types of land use change.

The International Tropical Timber Organisation (ITTO) estimated 8.5 million km^2 of degraded and secondary forest in 2000, similar to estimated from the FAO. With degraded forest covering 3.5 million km^2 and secondary forest covering 5 million km^2. The ITTO defined secondary forest as forest regrowing on land that was cleared of its original vegetative cover or recovering after selective logging. Another estimate by Pan et al. (2011), estimated that tropical regrowth forest covered and area of 5.6 million km^2 in 2007. In this context tropical regrowth forest was defined as forest regrowing on areas that had been deforested or selectively logged, and therefore corresponds with the ITTO estimate for 'secondary forest' cover. However, whilst these estimates give us an indication of the extent of degraded forest, the rate of forest degradation is still unclear.

1.4.2. Drivers of deforestation and forest degradation

Over the past few decades tropical forests have been threatened with large-scale land use change, impacting carbon storage, biodiversity and ecosystems services. The direct causes of deforestation and forest degradation include: timber extraction, agricultural expansion,

and mining (Figure 3). However, the underlying drivers of deforestation and forest degradation are more complex and often due to multiple factors (Geist and Lambin, 2002)

By far the largest cause of deforestation is agricultural expansion, in South America this is predominantly through conversion of forest to pasture for cattle ranching and for soya (*Glycine max*) cultivation, whereas in Africa timber extraction for fuelwood is a more common cause of deforestation (Geist and Lambin, 2002). Meanwhile, in Southeast Asia the rapid expansion of palm oil plantations over the past two decades has been the principal cause of deforestation (Miettinen et al., 2012).

Policy initiatives to increase economic development have had a large impact on forest cover in the recent past. The increasing value of timber on international markets and industrialisation of agriculture to produce crops for export, have been important underlying drivers of deforestation and forest degradation. (Rudel et al., 2009). DeFries et al. (2010) also noted an increase in deforestation related to agricultural exports and urban population growth, which led to an increased demand for food. However, this was not the case in Africa where a high urban population has been linked to lower deforestation rates, which has been attributed to large oils and mineral industries, which discouraged agricultural expansion (Fisher, 2010). Despite regional differences in the causes of deforestation and forest degradation, it seems that the increasing commercialisation of agriculture is becoming a dominant driver. This is a trend that could feasibly continue into the future with a growing population creating a greater demand for food and biofuel production.

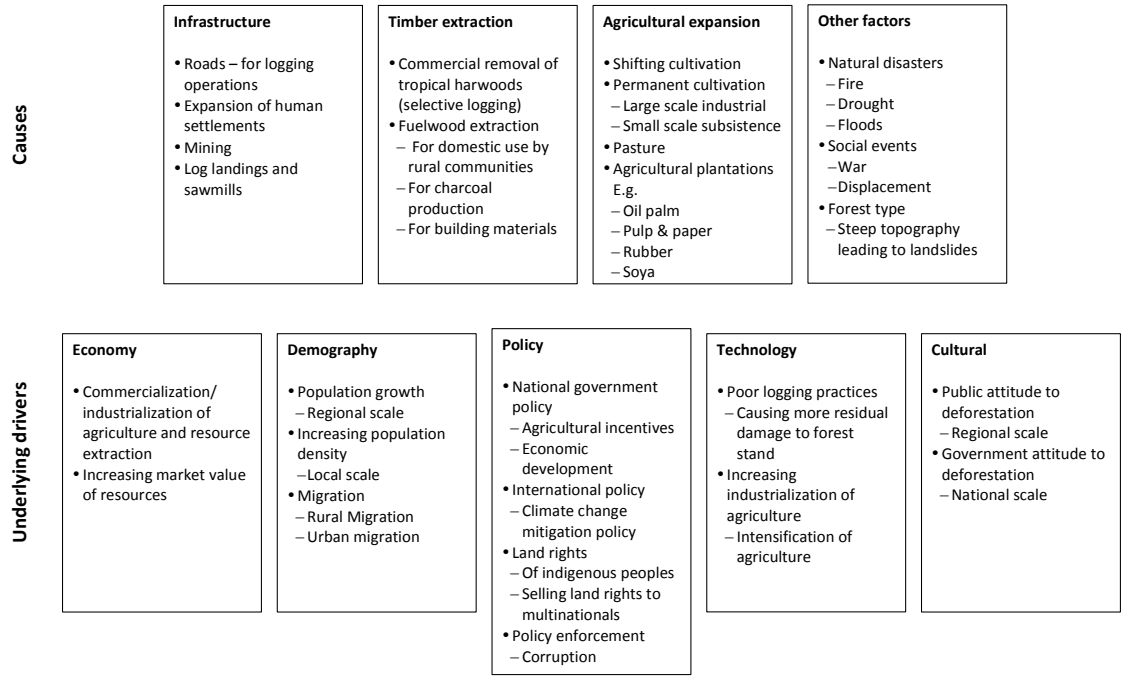

Figure 3. Explanation of the causes and underlying drivers of deforestation and forest degradation, adapted from Geist and Lambin (2002)

1.5. Impacts of deforestation and forest degradation

1.5.1. Impacts of deforestation and forest degradation on regulating services

1.5.1.1. Carbon sequestration and climate regulation

Tropical forests play an important role in the global carbon cycle storing >50% of terrestrial carbon (Pan et al., 2011) and cycling 120 Pg C yr^{-1} in GPP (Beer et al., 2010), meaning changes in forest extent can impact the global carbon cycle. The global carbon cycle is driven by the interactions and exchanges between the five major carbon pools, in decreasing size; the oceanic, the geological, (which contains fossil fuels), the pedologic (soil), the atmospheric and the biotic pools (Lal, 2008, Figure 4).

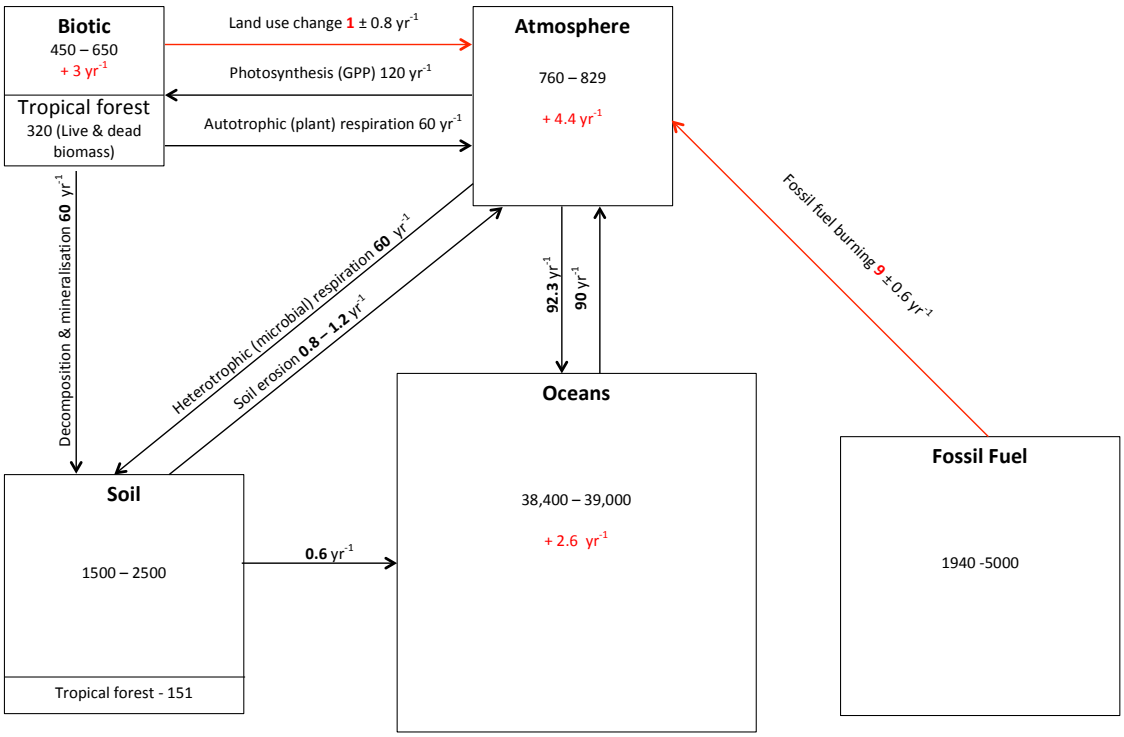

Figure 4. Diagram of the global carbon cycle showing major pools and fluxes (adapted from Lal, 2008). Values in boxes are carbon stocks (Pg C) from IPCC (2013) and Lal (2008). Size of boxes related to size of stock (not to scale). Stocks for tropical forest live and dead biomass and soil to 1 m taken from Pan et al. (2011). Carbon fluxes (alongside arrows, Pg C yr^{-1}) from IPCC (2013) and Lal (2008). Anthropogenic carbon fluxes (red arrows) and estimated sinks of anthropogenic carbon fluxes (red values in boxes) from (IPCC, 2013).

The carbon cycle is naturally a very dynamic system with large quantities of carbon transferred between pools (Figure 4). However, recent anthropogenic activities, since the start of the industrial revolution, have led to major changes in the exchange of carbon amongst these pools. This has led to an increase in atmospheric CO_2 concentrations, from 280 parts-per million (ppm), prior to the industrial revolution, to 400 ppm in 2014 (Le Quéré et al., 2015). The majority of anthropogenic carbon emissions originate from the geological pool, as a result of fossil fuel burning, and from the terrestrial pool, as a result of land use change, deforestation and soil erosion (Lal, 2008, IPCC, 2013).

This increase in carbon emissions has resulted in increased atmospheric CO_2 concentrations, which have a positive radiative forcing effect. Radiative forcing is the difference between radiant energy from the sun meeting the earth's surface, and the fraction of that energy that is reflected back to space. Greenhouse gasses, such as CO_2 block the emitted energy leaving the atmosphere, thereby increasing air temperature (IPCC, 2013). Therefore, understanding the magnitude of carbon fluxes, and the ability of different pools to store carbon, is important to understanding the effect that increasing atmospheric CO_2 concentrations can have on climate change. Leading on from this, developing methods to increase carbon pools can help mitigate the effect of climate change.

Annual anthropogenic carbon emissions are estimated to be 10 Pg C yr^{-1}, averaged between 2005 and 20014, with 9 Pg C yr^{-1} from fossil fuel burning and 1 Pg C yr^{-1} from land use change (Le Quéré *et al*., 2015, Figure 4). The oceans and terrestrial biomes act as a carbon sink, each sequestering 27% of emitted carbon, with the remaining 45% of emissions remaining in the atmosphere (Le Quéré et al., 2013). The current uptake of carbon into the oceans is estimated to be 2.6 Pg C yr^{-1} (Grace, 2004, IPCC, 2013, Lal, 2008, Le Quéré et al., 2015), increasing from 1.1 Pg C yr^{-1} in the 1960's (Le Quéré *et al.*, 2015, Figure 5). Approximately 4.4 Pg C yr^{-1} remain in the atmosphere. As with the ocean sink, the proportion of carbon remaining in the atmosphere has also increased since the 1960's (Figure 5) from 1.7 Pg C yr^{-1} (Le Quéré et al., 2015). Often the terrestrial carbon sink is calculated as the residual of the atmospheric and oceanic sinks (Malhi and Grace, 2000), and the Le Quéré *et al.*, (2015), estimate the remaining 3 Pg C yr^{-1} is take in by forests into the terrestrial sink via photosynthesis (Figure 4). There is also evidence to suggest that the terrestrial carbon sink has increased since the 1960's, from 1.7 Pg C yr^{-1}, however this

is subject to large interannual variability (Figure 5), which is sensitive to climatic events such as ENSO (Le Quere et al., 2009, Grace, 2004).

However, both the size and location of the terrestrial carbon sink is uncertain (Grace, 2004, Wright, 2013, Phillips and Lewis, 2014). Recent research efforts are helping to untangle some of the uncertainty surrounding the terrestrial carbon budget (Grace et al., 2014). Geographically, 55% of terrestrial carbon is located in tropical forests, 32% in boreal forests and the remaining 14% in temperate forests (Pan et al., 2011). In a study by Pan et al. (2011) tropical forests were divided into intact and regrowth forests. They estimated a large gross tropical carbon sink, between 1990 and 2007, of 2.8 Pg C yr^{-1}, split between intact forests (1.2 Pg C yr^{-1}) and regrowth forest (1.6 Pg C yr^{-1}). Once the emissions from deforestation (2.9 Pg C yr^{-1}) were removed, tropical forests became a small net source of 0.1 Pg carbon yr^{-1}.

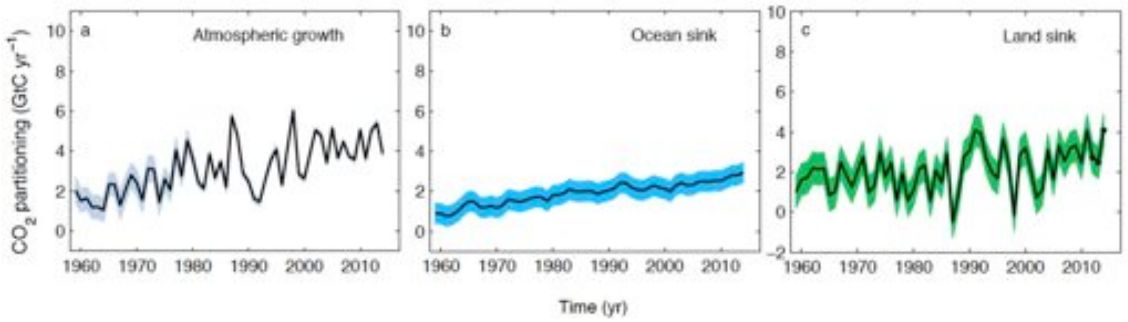

Figure 5. Change in carbon sink between 1960 and 2010 (Gt C yr^{-1}). a. atmospheric growth, b. ocean sink and c. land sink. Light blue, mid blue and green boundaries show 95% CI. Figures taken from Le Quéré et al. (2015).

Another study by Grace et al. (2014) also found tropical forest to be a small net source of 0.16 Pg C yr^{-1}, similar in magnitude to that of Pan *et al*, (2011), albeit with a large uncertainty of 1.1 Pg C yr^{-1} attached. They estimated a source of 2.1 Pg C yr^{-1} from tropical forest, balanced by a sink of 1.9 Pg C yr^{-1} (Table 8). They conclude that tropical forest could become a large carbon sink if emissions from deforestation and forest degradation were drastically reduced. These studies do not include the role that forest restoration could play in increasing the tropical terrestrial carbon sink, however, it is clear that the combination of reducing carbon emission, and enhancing terrestrial carbon storage could increase the terrestrial carbon sink, and help mitigate the effects of climate change.

Table 8. Tropical carbon fluxes as estimated in Grace et al. (2014). Positive values denote a source of carbon and negative values denote a sink of carbon.

Disturbance or forest type	Flux (Pg C yr^{-1})
Deforestation	0.93
Degradation	0.27
Harvest	0.34
Peat burning	0.54
Primary forest	-0.47
Secondary forest	-1.20
Plantations	-0.24
Net flux	**0.16**

1.5.1.2.Biodiversity protection

Deforestation and forest degradation in the tropics is often detrimental for biodiversity, leading to decreased species richness and changes in species abundance and altered species composition. Changes in species abundance include both reduced abundance of forest specialist or endemic species and increased abundance of generalist species. Such losses of biodiversity can have negative consequences on the regulating ecosystem services forests provide such as increased stability, increased productivity and ecosystem function and reduced invisibility by pests are reduced (see section 1.3.1.3.).

The magnitude of the effects that deforestation and forest degradation have on biodiversity is dependant on region, taxa and disturbance type. A meta analysis of 138 studies by Gibson et al. (2011) assessed the differences in biodiversity between old-growth forest and disturbed forest. They found that the impacts of disturbance on biodiversity were greatest in Asia, with an effect size of 0.95, much higher than seen in all other regions. Taxa responses were idiosyncratic, with plant and athropod diversity negatively effected by disturbance but, mammal diversity actually exhibited small positive effects to disturbance. The negative effects of disturbance on species richness were greater when just specialist species were considered, suggesting that specialist species do particularly poorly in disturbed habitats. In general Gibson *et al*, found that agricultural landscapes were the most detrimental for biodiversity, with plantations and agroforests having intermediate effects. They concluded that selectively logged forest could be important for biodiversity conservation

Another study by Barlow et al. (2007) also found idiosyncratic responses of different taxa to disturbance. They compared biodiversity of 15 taxa in primary forest, secondary forest and eucalyptus plantations in Amazonia. Eight taxa, including: trees, amphibians, birds, bats and butterflies had significantly lower species richness in secondary forest and plantations, five taxa including small mammals, flies and grasshoppers, had no significant difference in species richness between habitats, whilst moths had significantly higher species richness in secondary forest. Summed over all taxa, they found that secondary forests held 59% of primary forest species compared to plantations, which held 47% of primary forest species. Similarly, a review by Fitzherbert et al. (2008) assessed the impact of oil palm plantations on biodiversity. Of the 12 taxa assessed, all but one had lower species richness in oil palm plantations compared to old-growth forest, with species richness on average 77% lower in oil palm plantations.

Understanding the response of different taxa to disturbance is important if we are to fully understand the impact of biodiversity losses on ecosystem function. One of the main ways in which ecosystem function is altered by biodiversity loss is through ecological cascades (Gardner et al., 2009). Ecological cascade effects occur when the removal or population decline of a species leads to changes in the population of another species. For example Terborgh et al. (2001) found that the removal of predators from forested islands in Venezuela led to increases in herbivore density (including monkeys, rodents, iguanas and leaf-cutter ants), which in turn led to declines in seedling recruitment. Similarly changes in the density of frugivorous mammals, such as birds and bats, can have negative impacts on plant species which rely on animals for seed dispersal (Gardner et al., 2009). Effects such as this are worrying as decreased dispersal and germination will decrease regeneration in degraded forest.

1.5.1.3. Watershed protection

Land use change influences the watershed protection services forest provide by altering the natural flow of water within a catchment and reducing water quality. When forests are replaced by less complex vegetation, such as pasture grasses or agricultural crops, localised rainfall can increase over open areas. Following forest clearance, water-flow into streams can increase by an estimated 145 to 820 mm yr^{-1} (Bruijnzeel, 2004), due to a

reductions in stems who use water for photosynthesis. Indeed, increases in water-flow have been shown to be positively correlated with the proportion of biomass removed from a forest (Bruijnzeel, 2004).

Reductions in stem density also mean fewer trees are present to intercept rainfall, therefore, during wet periods soil quickly become saturated, and water flows as surface runoff more readily during heavy rainstorms, potentially leading to localised flooding. This effect is exacerbated by the compaction of soil in disturbed forest (See section 1.3.1.5.). Water infiltration is lower in more highly compacted soils, such as those associated with agricultural pastures and skid trail in logged areas, infiltration is much lower (Martínez and Zinck, 2004) therefore water runoff is much higher, flowing directly into streams (Bruijnzeel, 2004, Bruijnzeel, 1990).

Water quality is also affected by land use change. Conversion of tropical forest to agricultural land increases the risk of pollutants running off into streams and rivers (Uriarte et al., 2011). Agricultural expansion and the increasing industrialisation of agriculture has led to widespread use of pesticides and fertilizers, these can then run off into watercourses as surface water or by leaching into the groundwater (MEA, 2005). Pesticides and fertilizers can cause many problems for water quality, chiefly via eutrophication and algal blooms, which deplete dissolved oxygen found in water, in turn killing native fauna (MEA, 2005).

1.5.1.4.Soil protection

The presence of tropical forest can help reduce soil erosion and siltation. However, the removal of forest leads to rapid erosion of soil, as topsoil is washed away by heavy rainfall. A study by Ehigiator and Anyata (2011) measured soil erosion in areas cleared of original forest cover using different manual and mechanical clearance methods. They found that increased mechanisation led to increased sediment load in water, with negligible soil erosion in primary forest and 2.5 tons ha^{-1} of soil erosion into water in manually cleared areas. However, in intensively mechanically cleared areas soil erosion into water increased to 17.5 tons ha^{-1}. They concluded that increased erosion was a result of increased soil compaction in more heavily degraded areas and the removal of roots reducing soil stability. These findings are particularly significant when you consider that

erosion generally remove topsoil from an area, and it is topsoil that contains the highest concentration of nutrients and seeds, which are required if forest are to recover after clearance.

Higher sediment load in streams and rivers, can also increase nutrient load in water, alter freshwater species assemblages and change stream and river channels. A study by Iwata et al. (2003) assessed differences in stream characteristics and biodiversity in old-growth and secondary forests in Sarawak, Malaysia. They found that secondary forest streams had more heavily eroded banks and larger sediment deposition areas than old-growth forest streams, due to higher volumes of sediment in water, and these differences led to decreased diversity of benthic communities in secondary forest. Increased sediment suspended in water can also have implications further downstream as it is carried along watercourses, potentially causing modification to river channels and build up of sediment on the riverbed (Douglas et al., 1993). This is particularly noticeable in agricultural areas located on floodplains that depend of river flow to irrigate crops. For example, increased silt deposits within paddy fields in Sabah, Malaysia, raised their ground level, meaning that irrigation channels were not high enough to allow water to flow into all fields (Douglas et al., 1993), which could have implication for crop production. These combine effects demonstrate the importance of maintaining the soil structure found in natural tropical forest ecosystems.

1.5.2. Impacts of deforestation and forest degradation on provisioning services

1.5.2.1. Timber

Timber production is an important provisioning service of tropical forests. Using conventional logging techniques trees are felled and remove them from the forest along skid trails using bulldozers (Whitmore, 1984), however, there are large regional differences in the volume of timber extracted. Both Africa and the Americas have relatively low timber extraction rates, at 13 m^3 ha^{-1} and 35 m^3 ha^{-1} respectively, compared to

Southeast Asia, which has a the highest timber extraction rate globally of 115 m^3 ha^{-1} (Martin et al., 2015). Limited planning prior to logging means that the residual stand is damage, this is particularly detrimental in Southeast Asia where an estimate 48% of the remaining trees are damage (Martin et al., 2015), and skid trails can traverse between 30-40% of the logged area (Pinard and Putz, 1996). Damage to the residual stand is much lower in Africa and the Americas with 15% and 28% of trees damaged following logging, respectively (Martin et al., 2015).

Such high levels of timber extraction, particularly in Southeast Asia mean the logging industry is currently very unsustainable. A meta-analysis of 59 studies by Putz et al. (2012), assessed the sustainability of timber yields following selective logging. Studies had an average logging cycle of 29 years (± 2 years 95% CI), and a mean minimum cutting diameter of 54 cm (± 5 cm). They found that an average 35% (± 12.5%) of the original timber stock extracted, was available in the second round of logging, suggesting that the sustainability of timber yields and subsequent profits were limited. They suggested that maintaining timber yields would require; reducing logging frequencies, increasing minimum cutting diameters, applying silvicultural techniques after logging, such as cutting of vines and lianas, and finally using reduced impact logging (RIL) techniques to reduce damage to the residual forest stand (Putz et al., 2012).

RIL helps increase the sustainability of logging by planning the location of skid trails and using directional felling so fewer trees are damaged in the logging process. This means the residual stand retains higher stem density and therefore higher AGB following logging. A study by Pinard and Putz (1996) in Sabah, Malaysia, showed that areas logged using RIL techniques had 88 Mg ha^{-1} higher AGB than areas logged using conventional techniques one year after logging, with a total AGB of 264 Mg ha^{-1} and 176 Mg ha^{-1} respectively. RIL techniques also help ameliorate some of the other negative outcomes of conventional logging on ecosystem services such as minimising compaction and removal of soils and retaining biodiversity (Putz et al., 2008, Putz et al., 2000).

1.5.2.2.Non timber forest products

Deforestation and forest degradation has two major impacts on NTFPs; firstly by reducing availability following disturbance. This includes both reductions in the density of plant

species important for food and medicine, and reductions in the population density of game species used as bush meat. Secondly, by reducing access to lands were NTFPs are harvested due to the presence of commercial logging or agricultural enterprises. This means that following disturbance the extraction of NTFPs that grow naturally in tropical forest ecosystems is often severely reduced. A study by Rist et al. (2012), reviewed the effects of selective logging on NTFPs. They noted that the effects of logging on NTFPs were highly species specific with forest specialist species often reducing in abundance whilst species adapted to disturbance increased in abundance. Of the 38 studies they found, just 5% of studies recorded positive impacts of logging on NTFPs. One of these studies by Ashton et al. (2001) found that selective logging led to and increase in rattan (*Calamus zeylanicus*) density from 2 stems ha^{-1} to 10 stems ha^{-1}, this is a species which favours more open habitats therefore and increased in abundance due to increased light availability could be expected. However the negative impacts of selective logging on the abundance of NTFPs were far more apparent particularly in forest specialist species, with 82% of studies reported reduction in the abundance of NTFPs.

A case study site from Rist et al. (2012), located in Para, Brazil monitored the changes in availability of NTFPs used for food, construction and medicine, 10 years after selective logging. For the 12 species assessed there was an average 73% decline in NTFP resource abundance, which reduced availability. It has been suggested that for sustained availability of NTFPs, integrated management of land for both timber and NTFPs should be undertaken. RIL techniques have been suggested as a possible way of achieving this as it leaves a more intact residual forest stand which should also provide a greater availability of NTFPs of livelihood importance (Guariguata et al., 2010).

1.5.3. Impacts of deforestation and forest degradation summary

Clearly deforestation and forest degradation has a huge impact on ecosystem services provided by tropical forests from a global to local scale. Firstly, widespread forest loss in the tropics releases 2.9 Pg C yr^{-1} into the atmosphere (Pan et al., 2011), having a direct impact on the global climate, however, these emissions are largely offset by sequestration in intact and regrowth forest.. Deforestation and forest degradation also alters tropical forest hydrological and soil properties. An increase in incident rainfall can increase

surface water runoff (Bruijnzeel, 2004), and soil erosion (Ehigiator and Anyata, 2011), which can increase the risk of floods and decrease soil nutrients.

Deforestation and forest degradation also causes losses of biodiversity as a result of habitat loss and fragmentation. Fragmentation leads to isolation of populations, which can reduce species abundance, genetic diversity and cause localised extinctions (Laurance et al., 2011). Finally deforestation and forest degradation reducing the availability of resources derived from forests including timber, fuelwood, and NTFPs (Rist et al., 2012).

However these widespread negative impacts of deforestation and forest degradation are not necessarily permanent. It is possible to reverse their impacts and improve ecosystem services and ecosystem function by expanding forest cover. There are many ways in which forest cover can be expanded, with each method providing different ecosystem service benefits.

1.6. Land use change in the tropics: expanding forest cover

Expanding forest cover is currently the subject of much international attention due to the benefits associated with carbon sequestration. However, the different techniques available for expanding forest cover can have other beneficial outcomes such as: enhancing biodiversity, improving ecosystem services, producing financial or livelihood benefits for rural people and restoring specialist habitats such as a riverine areas (Lamb et al., 2005, Chazdon et al., 2015). Most methods for expanding forest cover fall into one of two categories, either afforestation and reforestation or forest restoration. Afforestation and reforestation are defined respectively as, the planting of trees on non-forest lands and the replanting of trees on land that was forest <10 years previously (FAO, 2000). Forest restoration is the rehabilitation of deforested or degraded lands, which have been abandoned, in order to recover some elements of forest structure and function.

In addition to expanding forest cover, reducing the impact of degrading activities so the residual stand retains more carbon (e.g. RIL) or protecting existing forest from deforestation and forest degradation have been proposed as methods to increase terrestrial carbon storage (Venter et al., 2012). Whilst these two options are not strictly carbon enhancing activities, they are both possible ways to reduce land use change emissions, however, they are not discussed in further detail in this review. The biodiversity co-benefits of different restoration strategies is not fully understood. However, it is clear that some restoration options would be far more beneficial for biodiversity than others (Lamb et al., 2005, Chazdon, 2008). The carbon and biodiversity outcomes of forest restoration and the likelihood of different techniques being employed are generally dependent on land managers and stakeholders desired outcomes, relative to the associated cost of restoration (Venter et al., 2012). Here the different options for expanding forest cover and the associated benefits for carbon and biodiversity are discussed and are summarised inTable 9.

Table 9. Summary of different restoration options and the associated cost, timeframe, C sequestration and biodiversity benefits and balance of services for each option.

Option to expand forest cover	Description	Primary purpose	Cost	Timeframe (years)	Carbon sequestration	Biodiversity enhancement	Balance of services
Afforestation & reforestation							
Monoculture plantation	Planting of single fast growing timber species E.g. Eucalyptus Spp., Acacia Spp.	Provisioning - timber Regulating - carbon storage	Medium	20-40 [a]	Medium	Low/Medium[e]	✓ Timber production high x Non-permanent C store as timber is cut
Polyculture plantation	Planting of two of more fast growing timber species E.g. Eucalyptus Spp., Acacia Spp.	Provisioning - timber Regulating - carbon storage	Medium	20-40 [a]	Medium	Low/Medium[e]	✓ Timber production high x Non-permanent C store as timber is cut
Agroforestry	Inter-planting forest with crops or planting of shade crop within agricultural area	Provisioning - food, fuelwood, NTFPs	Low	20-40 [a]	Low/Medium[d]	Medium	✓ Increases carbon and biodiversity in agricultural setting ✓ Reduced pressure on forest x Only subsistence scale
Forest restoration							
Enrichment or restoration planting	Planting of many different native tree species	Regulating service - C sequestration, climate regulation, biodiversity protection	High	100+ [b]	High	High	✓ Restore forest old-growth state x Extremely costly x Long timeframe
Assisted natural regeneration	Removal of undesirable spp.	Regulating service - C sequestration, climate regulation, biodiversity protection	Medium	100+ [b]	High	High	✓ Restore forest old-growth state x Costly x Longer timeframe than enrichment planting
Assisted natural regeneration	Fire protection	Regulating service - C sequestration, climate regulation, biodiversity protection	Medium	100+ [b]	High	High	✓ Restore forest old-growth state ✓ Prevents fire x Costly x Longer timeframe than enrichment planting
Natural regeneration	Protecting area of degraded forest to allow them to recover naturally	Regulating service - C sequestration, climate regulation, biodiversity protection	Low	100+ [c]	High	High	✓ Restore forest old-growth state ✓ Low cost x Longer timeframe than enrichment planting x May have arrested succession

a = average rotation length of plantation, b = value taken from results presented in chapter 3 , c = Martin et al. (2013), d = carbon sequestration potential of agroforests dependent of types of crops planted and length of cutting cycle, e = biodiversity benefits of monoculture and polyculture plantations are dependant on management,

1.6.1. Afforestation and reforestation

1.6.1.1.Monoculture and polyculture timber plantations

Timber plantations offer good potential for carbon storage and provisioning services, however, biodiversity benefits are limited as plantations replace areas with a small number of non-native timber species that will eventually be removed and sold. The area of tropical timber plantations is vast, estimated at between 90 million ha in 2005 (FAO, 2009) and 140 million ha in 2010 (FAO, 2010), meaning they are an important source of timber. Plantations can also attain relatively high carbon density at maturity, with maximum above ground carbon (AGC) estimates of 200 Mg C ha^{-1} (Ziegler et al., 2012).

This means that timber plantations can offer good carbon storage benefits at a landscape level, if managed properly on a rotational basis, with carbon losses from localised felling, being offset by planting of new plantations in other areas. However, caution over the carbon benefits of plantation is needed, particularly if plantations replace natural forest cover, which are estimated to have a maximum AGC of 400 Mg C ha^{-1} in the same study by Ziegler et al. (2012).

Monoculture plantations are dominated by fast growing *Eucalyptus* spp., *Acacia* spp. and *Pinus* spp, with estimated AGB accumulation of 10 Mg ha^{-1} yr^{-1}, often planted in short rotation cycles of less than 20 years (Bonner et al., 2013). However, timber plantations are detrimental for biodiversity, reducing species richness by an estimated 35%, when replacing native habitats (Bremer and Farley, 2010) Of particular note is the effect of oil palm plantations on biodiversity. Oil palm plantations alone cover 17 million ha, 70% of which are located in Malaysia and Indonesia (FAOSTAT, 2014), and have much lower AGC storage than timber species estimated at just 69 Mg C ha^{-1} (Ziegler et al., 2012), suggesting that their carbon benefits are minimal. There have also been multiple studies showing the detrimental effect that oil palm plantations can have on the biodiversity of forest specialist species such as; reduction in species richness and abundance and increased abundance of habitat generalists (E.g. Edwards et al., 2010, Brühl and Eltz, 2010, Fitzherbert et al., 2008, Peh et al., 2006). For example, a study by Edwards et al. (2010) monitoring bird biodiversity in oil palm plantations found species richness was 75% lower in plantations compared to old-growth forest.

Polyculture plantations involve the planting of two or more timber species, and can include a mixture of native and exotic species (Venter et al., 2012). Polycultures require more maintenance than monocultures due to the presence of different species with different requirements (Lamb, 2010), however, they do pose greater carbon and biodiversity benefits. Polyculture plantations are more productive than monoculture plantations due to a more complete utilisation of resources by different species present (Erskine et al., 2006). A study by Kanowski and Catterall (2010) conducted in Australia, found an average AGB of 62 Mg C ha^{-1} in monocultures, compared to 83 Mg C ha^{-1} in polycultures. Different species within a polyculture plantation may also have different harvest cycles meaning that plantation are not fully cleared of trees after harvest, meaning more carbon is retained in the landscape.

1.6.1.2.Agroforestry

Agroforestry is an agricultural system that involves either the interplanting of crops with trees to provide food (fruit trees) and timber, or the planting of crops (such as coffee) under a natural foresdt canopy (Lamb, 2010). Agroforestry uses multi-strata planting to combine several native and exotic crop and timber species within a single area. Although agroforestry is not strictly an afforestation and reforestation option, it does lead to increased tree cover within an agricultural setting whilst offering additional benefits for biodiversity and provisioning services by producing NTFPs and fuelwood (Albrecht and Kandji, 2003). This is particularly important in light of the rapid rural population growth in many biodiverse regions of the tropics (Cincotta et al., 2000), which puts increasing pressure on remaining forest. Agricultural practices that increase carbon storage in comparison to traditional cultivation methods and increase biodiversity, whilst providing livelihoods for rural people should therefore be seen as a 'win win' situation.

Agroforestry systems have much higher carbon storage values, of up to 100 Mg C ha^{-1}, compared to areas under permanent cultivation with AGC of 15 Mg C ha^{-1} (Ziegler et al., 2012). Another study by Albrecht and Kandji (2003) found that agroforestry systems stored between 12 and 288 Mg C ha^{-1} with a median value of 95 Mg C ha^{-1}. Both of these studies show the high carbon storage potential of agroforestry systems in comparison to traditional crops. However, by nature the AGC benefits of agroforestry are very variable, as in different regions, different crops are selected (Bhagwat et al., 2008). Carbon storage is dependent on the density of planting and the rotation length therefore appropriate management of agroforestry systems is needed to ensure long-term carbon storage.

The biodiversity benefits of agroforestry systems are also well documented. The diversity of trees in agroforestry systems can also lead to increases in faunal diversity (Venter et al., 2012). A study by Bhagwat et al. (2008) suggested that this was down to three main reasons. Firstly, at a landscape scale, agroforestry increases habitat heterogeneity due to the selection of species planted by different households. Even within a small region species selection among households differed leading to overall increases in species richness. Secondly, the presence of a tree canopy in agroforests allows species such as birds and bats, to travel through agroforests. Meaning agroforests may help protect

species outside of protected areas, acting as corridors for wildlife between forest fragments. Finally, the presence of trees within agroforestry systems reduces the pressure on protected areas and means that people living in surrounding areas are less dependent on forest for fuelwood, which can reduce degradation in old-growth forest. The combination of these factors means that the expansion of agroforests should be encouraged within agricultural landscapes as they offer far greater benefits for carbon and biodiversity than traditional cultivation methods.

1.6.2. Regeneration following deforestation and forest degradation

Following deforestation and forest degradation, cleared areas can undergo prolonged and intensive land use for many purposes (see Table 11.), if appropriate silvicultural or agricultural practices are employed. However, sustained productivity for many years is not always guaranteed. Poor land management practices or intensification of agriculture can lead to reduced productivity, reduced ecosystem services and reduced economic value (Sasaki et al., 2011). This often leads to abandonment of large areas of land, with agriculturalists and loggers moving on to other more productive areas. If left untouched, without human intervention, degraded and deforested lands that have been abandoned (hereafter termed abandoned land) can begin to naturally regenerate following the process of secondary succession (Visualised in Figure 6.). Natural regeneration of abandoned land leads to the recovery of biodiversity, restoration of ecosystem services and the accumulation of biomass and therefore carbon. Such carbon sequestration on abandoned land is seen by many as an important potential way of mitigating the effects of climate change by reducing atmospheric CO_2 (Lamb, 2010, Chazdon, 2008, Chazdon et al., 2016b).

The ability of an ecosystem to naturally regenerate following abandonment is dependent on a number of factors including; climate, edaphic conditions and the type of degradation experienced. Generally more severely degraded habitats, such as cattle pastures that have highly degraded soils and no tree cover, regenerate more slowly than habitats that have experienced less severe disturbance, such as areas selectively logged using reduced impact logging techniques, that minimise soil compaction and leave tree cover remaining.

For example a study by Uhl et al. (1988) compared AGB in pastures that had undergone light use (cleared and grazed) and heavy use (cleared, burned and bulldozed repeatedly), 8 years after abandonment. The AGB of light use pasture was 86.1 Mg ha^{-1} compared to 4.7 Mg ha^{-1} in heavy use pasture, suggesting that more heavily degraded pasture had a slower rate of recovery.

Not only the type of degradation but also, the duration of land use can influence recovery, with areas that have been under continuous used for many years recovering more slowly than areas that have been in use for a short time. A study by Hughes et al. (1999) measured AGB in secondary forest sites that had been under cultivation for between 1 and 30 years. They found an inverse relationship between AGB accumulation and duration of land use, with areas that had been in use for 1 year accumulating AGB at 13.5 Mg ha^{-1} yr^{-1}, compared to 4.3 Mg ha^{-1} yr^{-1} in areas used for 30 years. Nutrient poor soils often associated with heavily degraded areas can cause reductions in forest recovery rate (Buschbacher et al., 1988). Additionally, the climate of an area can impact forest recovery, with area of dry tropical forest generally recovering more slowly than areas of humid or wet tropical forest, due to water stress (Marin-Spiotta et al., 2008). The susceptibility of degraded areas to large-scale disturbance also influences recovery, with more heavily degraded areas being more prone to fire (Cochrane et al., 1999) or landslides in steep areas (Mugagga et al., 2012) hindering the natural regeneration of forest.

The recovery of abandoned lands has been well documented in the literature. Many studies document the rate of biomass accumulation, changes in forest structure and changes in biodiversity, following all types of forest degradation, across the tropics. There have been a few successful attempts to reconcile the literature to identify trends in the recovery trajectory of forests following disturbance, but generally these have been done for a particular region or for a single degradation type. For example, Poorter et al. (2016) assessed the recovery of secondary forest in the Neotropics estimating AGB accumulation of 6.1 Mg ha^{-1} yr^{-1} in the first 20 years after abandonment. Another meta-analysis of 47 studies by Bonner et al. (2013) estimated the rate of AGB accumulation in timber plantations and secondary forest regrowing after agricultural abandonment, finding faster AGB accumulation in plantations (10.8 Mg ha^{-1} yr^{-1}) than secondary forest (7.8 Mg ha^{-1} yr^{-1}) during the first 18 years of growth.

However, one of the overarching problems in the current literature is that the majority of research focuses on the accumulation of AGB in abandoned land following natural regeneration. There is a paucity of research examining how different management interventions might modify the rate of AGB recovery within abandoned lands. It is likely that active management could help accelerate the rate of AGB accumulation in abandoned lands, however, this has yet to be fully quantified, therefore the additional benefits of restoration on tropical forest recovery rates is still poorly understood. This is of interest for three main reasons. Firstly, there is currently a great deal of attention from the international community promoting the role of active forest restoration to mitigate climate change, by offsetting atmospheric CO_2 emissions from fossil fuel burning, and land use change (Lamb et al., 2005). Secondly, whilst in some areas abandoned land can naturally regenerates quite rapidly, in other areas natural regeneration is slow or halted altogether in a process termed arrested succession, meaning that without human intervention forest cover may not recover. Finally, aside from carbon sequestration, tropical forests provide numerous other ecosystem services, important for human wellbeing and normal ecosystem function. Ecosystem services can be severely diminished in abandoned land, however, management interventions that aim to increase AGB accumulation could also help the recovery of other ecosystem services (Figure 6).

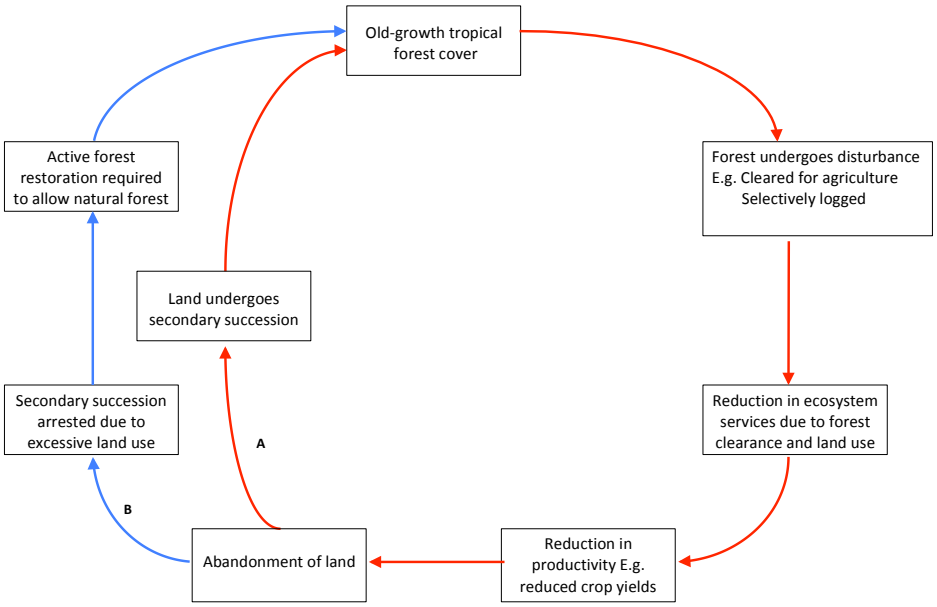

Figure 6. Diagram of the processes tropical forest undergo following disturbance. Route A shows area undergoing natural secondary succession, route B shows area experiencing arrested succession.

1.6.3. Processes of arrested succession

Recovery of abandoned lands generally follows the process of secondary succession, whereby habitats undergo a number of natural processes to regenerate back towards the structure and function of old growth forest. In areas that have been completely cleared of forest cover, once abandoned they initially become dominate by grasses and shrub species. This creates a harsh microclimate of high light and low soil moisture that few tropical forest tree species are adapted to survive in. These conditions are suitable for the germination and growth of 'pioneer' tree species that are light demanding and are able to grow in the harsh microclimate of early successional habitats (Guariguata and Ostertag, 2001). The rapid growth of pioneer trees creates a forest canopy, shading out grasses and shrubs. Tree cover allows for the movement of forest fauna such as birds and mammals into successional areas, enabling the dispersal of seeds from surrounding old growth forest.

This eventually leads to the colonisation and germination of old-growth forest specialist species (Finegan, 1996). These old-growth species eventually supersede pioneer species once gaps form in the forest canopy, often within a few decades - the average lifespan of pioneer trees (Guariguata and Ostertag, 2001, Rees et al., 2001). However, it can take well over one hundred years for the structural and floristic composition of successional forest to be comparable with old growth forest (Martin et al., 2013), depending on the severity of disturbance experienced within the area. However, in severely degraded habitats secondary succession can often be extremely slow or in some cases halted altogether, in a process termed 'Arrested succession'. Arrested succession tends to occur when multiple factors work in unison, creating complex barriers to natural secondary succession.

Table 10 Description of the different types of land use change causing deforestation and the associated benefits and problems

Land use change	Description	Benefits	Problems
Selective logging	• Selective removal of commercial valuable timber species over a set DBH cut-off. • Logged on rotational basis – typically 20-40 year rotation	• Tree cover remains • Biodiversity • Timber production • Carbon storage	• Residual stand severely damaged as: – Directional felling rarely used – Skid trails & log landings poorly planned • Rotation period between the 1st and 2nd logging often reduced • DBH cut-off reduced in the second logging
Shifting cultivation	• Rotational agriculture system • Small forest area cleared and often burnt • Planted with food crops for 2-3 years. • Land left fallow for few years to accumulate soils nutrients	• Continuous food production at subsistence level • Fallow period means low fertiliser requirements • Rotation between fields means limited encroachment into forest	• Increasing rural populations mean shorted fallow period & expansion • Leads to gradual depletion of soil nutrients • Reduction in crop yields • Encroachment into forest to access more productive land
Agriculture – crop production	• Few trees • Low diversity • Permanent cultivation of agricultural crops • In tropics mainly; cereals (maize, millet, sorghum), cassava, banana, tea, coffee, soya and rice	• Food production at commercial level • Profits for landowners	• Reduced yields year on year • Large fertiliser use – leaching into watercourse • Soil degradation – nutrient depletion • Lack of regeneration post abandonment
Agriculture – Cattle ranching	• Grassland habitat • Few trees • Low diversity	• Food production – Beef • Profits for landowners • Tax receipts to governments	• Invasion of grasses unpalatable to cattle • Soil degradation – compaction & nutrient leaching • Lack of regeneration post abandonment
Monoculture plantations	• Tree plantation of single species (E.g. Oil palm, rubber, eucalyptus) • Low diversity	• Produce timber, pulp & paper products, biofuel, palm oil • Profits to landowners • Store carbon	• Often replace naturally regenerating forest • Soil degradation • Susceptible to pests •
Agro forestry	• Agriculture system – crops interplanted with trees • Use many different crops and tree species • Intermediate diversity	Compared to other agricultural systems: • Higher biodiversity • Higher carbon storage • Help maintain soil fertility • More resilient to pests • Reduced need for herbicides and fertilizers • Reduce pressure on forest by providing fuelwood	• Predominantly practiced at subsistence level • Not feasible for large scale crop production

1.6.3.1.Fire

One of the most destructive forces impeding the recovery of degraded habitats is fire. The occurrence of fire in the tropics is thought to be increasing (Liu et al., 2010); rapid habitat fragmentation as a result of forest clearance allows fires to spread into forest from surrounding areas (Uhl and Kauffman, 1990), especially in agricultural areas where fire is used to clear land. Degraded habitats and forest fragments are more susceptible to fire, as reduced canopy cover and higher incident sunlight hasten drying of debris meaning fires can spread easily (Gerwing, 2002), (Cochrane and Laurance, 2002). Alongside this, major fire events associated with drought periods - such as the 1997-1998 El Niño Southern Oscillation event (Fuller et al., 2004) - increase fire susceptibility.

Initial fires in a forest are generally surface fires and appear to be less destructive, just burning the litter layer and small trees. However, surface fires are able to destroy tropical forest seedlings and many seeds stored in the leaf litter and topsoil inhibiting the regeneration of forests after fires and limiting succession (Cochrane, 2003). Tropical trees also typically have thin bark, meaning they have poor evolutionary adaption to fire and even low intensity fires can damage larger trees to a point were they are committed to mortality within a few years after a fire (Cochrane et al., 1999). Fire related mortality increases the fuel load in forests, creating a more open canopy with higher solar radiation, speeding up the drying of fuel (Gerwing, 2002). A more open canopy also leads to the invasion of grasses and herbs that are highly combustible (Cochrane, 2003). All of these factors combined create a positive feedback effect whereby, burnt forest are more susceptible to repeat burnings (Cochrane et al., 1999) which can severely diminish the ability of a forest to regenerate.

1.6.3.2.Seed bank and seed rain

Poor dispersal and low numbers of seeds present in degraded areas can impede regeneration (Holl, 1999). The survival of seeds within the soil seed bank is important for recruitment of new trees following disturbance. However, despite high seed densities seen in degraded forest (Dupuy and Chazdon, 1998), the survival of seeds in soils of degraded areas can be short-lived. In some cases it has been suggested seeds persist within the seed bank for as little as one year (Guariguata and Ostertag, 2001). Therefore, degraded areas

need continuous seed input from surrounding forest for successful regeneration. The effects of a reduce seed bank are exacerbated by the increased presence of fire in degraded habitats, which can reduce the number of seeds present in soil by up to 60% (Cochrane, 2003).

The short residency time of seeds in the soil seed bank means that the arrival of new seeds into an area is important for the regeneration of degraded areas. Seeds are dispersed either by wind or animals. Wind dispersed seeds are generally small so can be carried on the wind, and are produced in large numbers. The large number of seeds these species produce means they are good colonisers. However, small seeds have low energy reserves, meaning that unless seed germinate rapidly they will not persist for long periods and therefore compete poorly with other species (Rees et al., 2001).

Animal dispersed seeds are generally larger and therefore too heavy to be carried on the wind. Larger size means that seeds have larger energy reserves and therefore are longer lived and can lie dormant for prolonged periods. However, they are produced in much smaller numbers, as each seed requires a much greater energy investment from the parent tree. This can corresponds with longer time intervals between each reproduction period, for example, seeds from the family the Dipterocarpaceae from Southeast Asia (Appanah, 1993). Meaning that species that do not reproduce annually are likely to be underrepresented in the seed bank. This effect overall leads to a species trade off between colonisation ability and competition ability of seeds of different sizes (Rees et al., 2001).

In degraded habitats seed rain can be much lower than in old-growth forest and is often dominated by wind-dispersed seeds that often do not travel large distances from areas of surrounding forest. A study by Holl (1999) measured seed rain in old-growth forest and adjacent abandoned pasture in Costa Rica. They found that seed rain was much higher in old-growth forest than in pasture (average 1670 seed m^2 vs. 190 seed m^2 respectively). Furthermore, just 3 animal dispersed seeds per m^2 were seen further than 5 m from the forest edge. Another study by Cubiña and Aide (2001) found that seeds dispersed no further than 8 m into pasture, from surrounding secondary forest, with >99% of all seed collected found within 2 m of the forest edge. These studies demonstrate how limited seed rain can be in degraded habitats, leading to greatly reduced rates of secondary succession.

Animal dispersed seeds are very under represented in seed rain as few forest specialist species choose to pass through open areas of degraded forest, thus before large numbers of animal dispersed seeds can be dispersed into degraded areas some form of canopy cover is required (Zahawi and Holl, 2009). This means that in highly fragmented landscapes seed rain can be especially low as the distance to the nearest seed source in some fragmented landscapes can be very large, therefore few seeds will reach some areas. These dispersal limitations can limit regeneration in degraded land meaning that succession is slow.

1.6.3.3.Soil

Heavily degraded soils can also lead to arrested succession in degraded habitats, largely related to soil compaction and the removal of nutrients following degradation. Soil compaction is problematic following selective logging, due to areas being repeatedly traversed by bulldozers (Pinard & Putz, 1996) and in old pastures repeated trampling by cattle. Soil compaction can limit regeneration as seeds find it difficult to germinate, the seed bank in topsoil has often been removed and subsequent erosion of soil removes further seeds (Nussbaum et al., 1995). Seed rain is also rapidly washed off compacted surface soil before seeds have sufficient time to germinate (Nussbaum et al., 1995). Compacted soils have a higher bulk density than undisturbed soils, causing reduced water infiltration and increases soil penetration resistance making it harder for seeds to germinate and spread roots (Martínez and Zinck, 2004, Nussbaum et al., 1995).

In a study by Hattori et al. (2013) seedling were planted in undisturbed forest and in skid trails following logging in Sarawak, Malaysia. Seedlings planted in compacted soils had slower growth rates of roots, than seedling planted in undisturbed soil, resulting in a less developed root structure. This led to higher seedling mortality in compacted soils. A study by Martínez and Zinck (2004) measured bulk density and soil penetration resistance in pastures of different ages and old-growth forest in the Colombian Amazon. Despite pastures having a low cattle stocking density (<1 animal ha^{1-}), they found that both bulk density and soil penetration resistance increased significantly with pasture age, leading to slow regeneration of seedlings. Slow regeneration within such openings is highly problematic for regeneration, as areas of compacted soil cover large areas. Tropical pastures cover an estimated 11.3 million km^2 globally (Grace et al., 2014). And, in some

selectively logged areas, log landings and skid trails cover between 15- 50% of the logged area (Nussbaum et al., 1995, Hattori et al., 2013).

Soil nutrients are rapidly lost following degradation via soil erosion and nutrient leaching. Soil is less protected by canopy cover and root structures after degradation, therefore, it is more exposed to direct heavy rainfall resulting in rapid erosion (Davidson and Martinelli, 2009). The more severely degraded a site is then the greater losses of nutrients it experience. A study by Uhl et al. (1982) compared soil nutrient content in pastures that were manually cleared and pastures cleared with bulldozers. They found large differences in soil nutrients between manually cleared and bulldozed sites, particularly Nitrogen (N), which was 21 mg per 100 g soil and 145 mg per 100 g soil, respectively. N is an essential nutrient for plant growth therefore, reductions in N concentrations could limit regeneration (Vitousek and Sanford, 1986).

1.6.3.4. Invasive species

Another barrier to natural regeneration is the invasion of exotic species into disturbed areas. Invasive species have been recognised a major threat to global biodiversity and ecosystem function (MEA, 2005), being included as one of the Aichi biodiversity targets (target 9) set by the UNEPs Convention on Biological Diversity (CBD) (CBD, 2011). For a species to be considered invasive it must be able to; out compete native organisms, spread rapidly within its new environment, and harm the ecosystem in its introduced range (MEA, 2005). There are a number of different factors that impact the invasibility of habitats by exotic species (Lonsdale, 1999). Most importantly, in the context of tropical forest are the effects of species richness and disturbance.

Species richness has been recognised as an important barrier to the invasibility of a habitat to exotic species (Hobbs and Huenneke, 1992). One proposed mechanism for this is through niche partitioning. This theory was first put forward by Elton (1958) and suggests that more species rich habitats are more resistant to invasive species, as there is reduced resource availability for invasive species, and increased competition from native species. Empirical evidence supporting this theory within tropical forests is limited, however there is some evidence to suggest that invasive species can lead to declines in forest biodiversity. A study by Laurance et al. (2012) assessed the 'health' of 60 tropical

protected areas and determined reasons for declines in protected area health. They found that 50% of the protected areas studied were declining in health; this was partly attributed to increases in the abundance of exotic plants and generalist trees, and vines. These results could suggest that the presence of exotic and invasive species is increasing within old growth forest, which could ultimately influence the species composition within old-growth forest.

Reduced biodiversity is often associated with forest disturbance, therefore disturbed habitats are often more susceptible to invasion as there is increased resource availability for invasive species (Lonsdale, 1999). In disturbed habitats the ability of a species to colonise an area, and to withstand the harsh microclimate conditions can determine its success (Catford et al., 2012). Many invasive species were originally introduced, either intentionally or accidentally, for uses in agriculture or forestry. Often species are selected for particular plant traits, such as rapid growth, that can pre-dispose them to being good colonists (Catford et al., 2012). For example, Van Kleunen et al. (2010) conducted a meta-analysis of 117 studies comparing plant trait of 125 invasive species and 196 non-invasive species. They found that invasive species had plant traits, which led to better performance (including; increase photosynthetic rate and increased growth rate), in comparison to non-invasive species, suggesting that invasive species would be able to outcompete non-invasive native species. Furthermore, as invasive species are often associated with human activities, such as agriculture, they are often planted at high densities meaning they are over-represented within a landscape, which enables more rapid spread and dispersal (Catford et al., 2012). It is when invasive species become dominant over native species, that they become barriers to succession, out-competing native species and preventing natural regeneration.

1.6.3.5.Arrested succession summary

It can be seen that there are number of barriers that can limit natural regeneration and lead to arrested succession. However, it is rare for a single factor alone to result in arrested succession. Generally it is the interaction between different factors that have the largest impact. For example, following degradation a reduction in soil fertility and seed stores will occur, meanwhile degrading activities create more open habitats allowing for the invasion of species. These three factors combined increase the risk of fire, which in

turn further reduces soil quality and seed stores, which creates a cycle of continual degradation.

To overcome the problems associated with arrested succession requires management intervention to provide competitive release from invasive species, reduce the risk of fire and assist the regeneration of seedlings, which in turn will improve soil quality. The use of management interventions can help to restore degraded and deforested areas back to a more natural old-growth forest state, however, there are several methods of forest restoration and the type of restoration activity employed are dependent on the desired outcomes of land managers and the type of degradation an area has experienced (Chazdon, 2008, Lamb et al., 2005).

1.6.4. Active forest restoration

1.6.4.1. Natural regeneration

Natural regeneration is potentially the easiest and cheapest option for forest restoration (Table 9) as it just requires land to be left to recover naturally via secondary succession and therefore requires no management interventions (Lamb et al., 2005). Natural regeneration could potentially offer the full suite of ecosystem services provided by old-growth tropical forest as described in section 1.3., including large carbon and biodiversity benefits, if areas are given long enough to recover (Figure 8), however, there are a number of problems associated with this approach. Firstly, many areas of abandoned land are prone to arrested succession because of fire, invasive species, poor site conditions and harsh microclimate conditions (as described in detail in section 1.6.3.). Secondly, areas of degraded land that have been left to naturally regenerate are more susceptible to conversion to other land uses, such as plantations (Edwards et al., 2011). The diminished returns from the sale of timber and crops within such areas means conversion to other land uses that produce higher profit is common (Edwards et al., 2011).

Naturally regenerating forests have been shown to harbour high levels of carbon and biodiversity. For example, a study by Berry et al. (2010) compared AGB and species richness of nine taxa in old-growth forest and selectively logged forest, 18 years after

logging. They saw that after 18 years of recovery AGB of secondary forest was 177 Mg ha^{-1}, just 100 Mg ha^{-1} lower than seen in old-growth forest. They also found that declines in species richness from old-growth to secondary forest were on average just 10%. These results show the value of naturally regenerating forest for both carbon and biodiversity, however, strong governance of naturally regenerating areas is needed to prevent conversion to other land uses and realise the full carbon and biodiversity potential of naturally regenerating land. Furthermore, the need for forest restoration often arises because forests are not able to naturally regenerate and require some form of management intervention

1.6.4.2.Assisted natural regeneration

The simplest option to overcome arrested succession is to use assisted natural regeneration. This involves using different silvicultural techniques that help accelerate plant growth and reduce competition, as well as protecting areas from further disturbances particularly fire (Venter et al., 2012). Assisted natural regeneration (ANR) provides similar carbon and biodiversity benefits to natural regeneration (Figure 8). However, with the addition of silvicultural techniques, forest recovery can occur more rapidly, with only a small financial outlay (Table 9). Furthermore, when compared to more intensive restoration strategies such as enrichment planting the cost of ANR is considerably lower. It is possible that ANR could be of particular benefit in degraded areas that still have some tree cover but where normal regeneration is being arrested, meaning that some management intervention is required.

The silvicultural techniques most commonly employed in ANR are the liberation cutting of invasive grasses, shrubs or vines that compete for resources with native tree seedlings and tree girdling of unwanted species (Peña-Claros et al., 2008). Liberation cutting of invasive species provides competitive release for native species, allowing them to utilize resources more easily resulting in accelerated growth rates (Shono et al., 2007a). A study by Peña-Claros et al. (2008) monitored the growth rate of trees in areas that had undergone reduced impact logging (RIL), and compared this to areas that had undergone RIL and additional silvicultural management in the form of liberation cutting of lianas and girdling of unwanted woody species. They found that the addition of silvicultural

management led to faster growth rates in trees, which could lead to faster recovery of forest biomass.

ANR can not only help accelerate regeneration but also help prevent further degrading activities such as livestock grazing, timber removal and most notably protecting areas of degraded forest from wildfire (Shono et al., 2007a). Degraded areas are known to be more susceptible to fires (Cochrane, 2003, Cochrane et al., 1999), and the presence of fire can be extremely devastating in tropical forest that are ill adapted to recover after fire. The creation of firebreaks in degraded forest areas can halt the spread of fires and is a relatively cheap management strategy. A study by Omeja et al. (2011b) measure AGB and biodiversity in a grassland protected from fire for 32 years. These grassland areas were originally forest but were not recovering due to repeated burning. In areas protected from fire they found an AGB of 30 Mg ha^{-1} and found a total of 46 different tree species, which suggests that protecting areas from fire can allow for the natural regeneration of forest cover and offers potential benefits for both carbon and biodiversity. Such simple measures can sometimes be sufficient to overcome the problems limiting natural regeneration. However, in very heavily degraded areas more intensive restoration activities are sometimes required.

1.6.4.3.Ecological restoration

Ecological restoration involves enrichment planting of degraded or deforested areas with native species, with the aim of restoring areas back to an old-growth forest state, restoring not just AGB but also biodiversity and the full suite of ecosystem services provided by old-growth tropical forest (Lamb et al., 2005, Kanowski and Catterall, 2010). Because of this, ecological restoration is seen as a particularly good option for restoring severely degraded lands that are experiencing arrested succession. Nevertheless, ecological restoration is also used for the restoration of areas that have been selectively logged, particularly in areas that have experienced very intensive logging. However, it is also the most costly method of restoration that requires large financial investment to be achieved (Chazdon, 2008). Enrichment planting involves the planting of different native tree species, many of which are pioneer species, within an area of degraded or deforested land, to allow a canopy of native trees to grow, accelerating the process of natural regeneration (Venter et

al., 2012). This has the potential to mimic natural secondary succession dynamics eventually offering carbon and biodiversity benefits similar to old-growth forest.

This process requires careful selection of tree species with suitable plant functional traits that are able to survive in the open conditions found in abandoned land. There have been a number of studies that have assessed the suitability of tree seedlings for restoration by monitoring seedling growth and mortality (E.g. Shono et al., 2007b, Kuaraksa and Elliott, 2013, Hooper et al., 2002). All of these studies concluded that for successful restoration, site-specific selection of species is required as some species are far more successful than others, suggesting that preliminary experimentation to determine appropriate species will increase the success of restoration. This obviously requires a great deal of knowledge about individual species life history traits, and time to determine appropriate species.

In addition to this, many other activities are required for enrichment planting to be implemented. Nurseries must be established to propagate seedlings for planting. Ground preparation in the areas to be planted is needed. Planted seedlings must be tended and monitored after plating to ensure survival. Staff must be trained to ensure activities are done properly. The combination of all these activities is costly, meaning that successful enrichment planting is an expensive and risky restoration method (Chazdon, 2008).

However, the benefits enrichment planting present for biodiversity and carbon sequestration could be sizeable. A study by Edwards et al. (2009) compared the biodiversity of birds in old-growth forest against selectively logged forest that was naturally regenerating and selectively logged forest that had received enrichment planted forest 15 years earlier. They found that species richness was not significantly different between restored and old-growth forest. However, naturally regenerating forest had significantly lower species richness than restored forest, suggesting that enrichment planting is a successful method of restoring biodiversity to degraded forest. However this restoration project was in areas of selectively logged forest and therefore this area may have retained high bird diversity, it is not as clear what the effects of enrichment planting of more severely degraded habitats (e.g. abandoned cattle pasture) would be on biodiversity.

The carbon sequestration benefits of enrichment planting could also be large if restored areas achieve old-growth forest AGB as has been suggested (Lamb, 2010). However, the evidence to back up these claims is noticeably lacking with very little literature showing the long-term carbon sequestration potential of enrichment planting projects. This is rather concerning as enrichment planting is one of the main methods being suggested by the UNFCCC to enhance forest carbon stocks under the future REDD+ mechanism (IPCC, 2014, see Section 1.8.).

1.6.4.4.Restoration studies – a synthesis

To gain a clearer understanding of the current state of restoration research I undertook a review of forest restoration literature specifically focusing on enrichment planting restoration research. I conducted a literature search using Web of Science database using the search term (tropic* AND forest* AND restor*). The resulting papers were included in this review if they; 1) were conducted in a region where the end point of succession was expected to be closed canopy tropical forest, 2) studies employed a specific restoration strategy, 3) studies reported change over time for one of AGB, forest structure (e.g. stem density, stem height, DBH) or biodiversity (e.g. species richness or abundance) and 4) studies presented original data and were not reviews of previously published data.

A total of 48 studies met these criteria, detailed in Table 11. These were very unevenly distributed across the tropics, with research being predominantly in Latin America (n=34). Across the rest of the tropics, just six studies were from Asia, five from Australia and three from Africa (Table 11), one of which was my own research conducted in Uganda (presented in chapter 3 of this thesis). Research was also heavily dominated by restoration of deforested land, with 92% (n=44) of studies conducted in areas that had been deforested for either; agriculture, pasture or a combination of the two. Just 8% (n=4) of studies were conducted in degraded land, which here refers to selectively logged forest. This suggests that degraded land, which covers a large area of the tropics and includes land uses other than selective logging such as abandoned agricultural fallows, is very under-represented in the current restoration literature.

Table 11. Summary of tropical forest restoration literature.

Type of Degradation	Country	Experiment type *a*	Treatment *b*	Control *c*	Response variable (AGB/ Structure/ Diversity) *d*	Years Restored (at time of study)	Area sampled (ha)	Number of species used	Natural regeneration
Agriculture	Brazil (1)	NA	NA	N	Diversity	10	ND	40	Y
	India (2)	Sequential	Sp./x/-cut/Habitat	N	Structure	2	3.65	27-82	N
	Panama (3)	Sequential	Sp./Cut freq	2	Structure	1	0.04	20	N
	Singapore (4)	Sequential	Density/Sp.	N	Structure	3-6	2	11 - 31	N
	Singapore (5)	Sequential	Planted	N	Diversity	1-4	0.6	30	Y
Agriculture then pasture	Australia (6)	Chronosequence	Planted	1	Diversity	1-24	0.3-5.8	20-50	Y
	Australia (7)	Sequential	Density/Sp.	N	Structure	5	3.32	6	N
	Australia (8)	Chronosequence	Density/Sp.	1	Structure	6 - 22	8.1	ND	N
	Australia (9)	Chronosequence	Sp.	1	AGB	5-20	2.65	9 - 14	N
	Brazil (10)	Sequential	Sp.	N	Structure	2	0.1	15	N
	Costa Rica (11)	Sequential	Sp./seedVcut	N	Structure	3	0.41	10	N
	Costa Rica (12)	Sequential	Sp./+/-fert	2	Structure	8	2.5	7	N
	Costa Rica (13)	Sequential	Density	N	Structure	8-9	12	4	N
	Costa Rica (14)	Sequential	Density	1	Diversity	3	4	4	Y
	Costa Rica (15)	Sequential	Sp.	N	Structure	7	0.45	7	N
	Mexico (16)	Sequential	Fert conc.	2	Structure	15	0.54	5	N
	Mexico (17)	Sequential	Fert conc.	2	ND	1	0.45	3	N
	Mexico (18)	Sequential	Sp.	N	Structure	4	0.04	25	N
	Mexico (19)	Sequential	Sp.	N	Structure	4	0.04	25	N
	Mexico (20)	Sequential	Habitat	N	Structure	0.5	0.03	6	N
	Panama (21)	Sequential	Sp./Habitat	2	Structure	2	19	49	N
	Panama (22)	Chronosequence	Sp.	N	AGB/ Structure	12	0.14	16	N
	Panama (23)	Sequential	Sp./+/-fert	2	Structure	7	2.5	3	N
	Uganda (24)	Sequential	NA	N	AGB	10	4	5	Y
	Uganda (25)	Sequential	Fire	N	AGB	12 - 32	1	0	Y
	Uganda (Chapter 2)	Sequential	NA	N	AGB	18	3.75	37	Y
Pasture	Australia (26)	Sequential	Sp./+/-fert	N	Structure	2	0.14	31	N
	Brazil (27)	Sequential	Sp./mecVman	N	Structure	1	0.24	14	N
	Brazil (28)	Sequential	Habitat	1	Structure	1	0.02	11	N
	Brazil (29)	Chronosequence	Sp.	N	Structure	5-10	0.81	38-42	Y
	Brazil (30)	Sequential	Sp./Habitat	1	Structure	1	0.05	3	N
	Brazil (31)	Sequential	Density/Sp.	N	Structure	19	5	8 - 14	Y
	Brazil (32)	Sequential	NA	N	Structure/ Diversity	1	ND	8	Y
	Brazil (33)	Sequential	Density/Sp.	N	Structure	9	9	42-95	N
	Brazil (34)	Sequential	Sp./Cut area	2	Structure	4	0.11	7	N
	Brazil (35)	Sequential	Sp./+/-fert	1	Structure/ Diversity	9	3.84	18	Y
	Costa Rica (36)	Sequential	Sp./Habitat	N	Structure	7	8.64	6	N

Type of Degradation	Country	Experiment type *a*	Treatment *b*	Control *c*	Response variable (AGB/ Structure/ Diversity) *d*	Years Restored (at time of study)	Area sampled (ha)	Number of species used	Natural regeneration
Pasture	Mexico (37)	Sequential	Sp./+/-fert	2	Structure	1	0.09	3	N
	Mexico (38)	Sequential	Sp.	N	Structure	0.8	0.12	2	N
	Mexico (39)	Sequential	Sp.	N	Structure	7	0.22	14	N
	Mexico (40)	Sequential	Sp.	N	Structure	2-9	0.15	4	N
Selective logging	Brazil (41)	Sequential	Sp.	N	Structure	8-16	ND	7	N
	Malaysia (42)	Sequential	Sp./+/-fert	2	Structure	0.5	0.004	4	N
	Thailand (43)	Sequential	Sp./seedVcut	N	Structure	0.25	1.62	6	N
	Vietnam (44)	Chronosequence	Sp.	N	Structure	2.5-9.5	8	7	N
Mining	Brazil (45)	Sequential	Sp./+/-fert	2	Structure	3	0.18	5	N
	Venezuela (46)	Sequential	Sp./+/-fert	2	Structure	0.75	0.16	5	N
Shifting Cultivation	Mexico (47)	Sequential	Sp./Habitat	N	Structure	7-8	0.02	3	N
	Mean (95% CI)					6.2 (1.5)	2.5 (1.1)	15.2 (4.4)	
	Median					4.8	0.5	7	

Data show; type of degradation, location of study, *a* = experiment type, studies either used sequential sampling of plots or forest chronosequences, *b* = experimental treatment method used in study, explanation of codes used in Table 12. *c* = use of controls N = no control, 1 = non-planted control, 2 = non-treated control i.e. compared fertiliser treatment with non-fertiliser control treatment. *d* = type of response variable AGB = AGB measured, structure = measured one of seedling DBH, height or basal area, diversity = some form of diversity indices or species richness measured, number of years restored when area was sampled, area surveyed in study (ha), number of species used for restoration and if natural regeneration was investigated (Y or N). Each line corresponds to single study. ND = No data available. NA = Not applicable to study. Sources: (1) Barbosa and Pizo (2006), (2) Raman et al. (2009), (3) Hooper et al. (2002), (4) Shono et al. (2007b), (5) Shono et al. (2006), (6) Catterall et al. (2012), (7) Grant et al. (2006), (8) Kanowski et al. (2003), (9) Preece et al. (2012), (10) Chaer et al. (2011), (11) Zahawi and Holl (2009), (12) Carpenter et al. (2004b), (13) Holl et al. (2011), (14) Zahawi et al. (2013), (15) Carpenter et al. (2004a), (16) Allen et al. (2005), (17) Barajas-Guzmán and Barradas (2011), (18) Martínez-Garza et al. (2005), (19) Martínez-Garza et al. (2013), (20) Perez-Hernandez et al. (2011), (21) Breugel et al. (2011), (22) Delagrange et al. (2008), (23) Plath et al. (2011), (24) Omeja et al. (2011a), (25) Omeja et al. (2011b), (26) Doust et al. (2008), (27) Bruel et al. (2010), (28) Camargo et al. (2002), (29) de Souza and Batista (2004), (30) Guarino and Scariot (2012), (31) Sansevero et al. (2011), (32) Leitão et al. (2010), (33) Massad et al. (2011), (34) Pereira et al. (2013), (35) Sampaio et al. (2007), (36) Calvo-Alvarado et al. (2007), (37) Nunez-Cruz and Bonfil (2013), (38) Ortega-Pieck et al. (2011), (39) Román‐Dañobeytia et al. (2012), (40) Pedraza and Williams-Linera (2003), (41) Keefe et al. (2009), (42) Nussbaum et al. (1995), (43) Kuaraksa and Elliott (2013), (44) McNamara et al. (2006), (45) Dias et al. (2012), (46) Fajardo et al. (2013), (47) Bonilla‐Moheno and Holl (2010)

Table 12. Description of different planting methods tested in restoration literature presented in Table 11.

Experimental method	Description	Code
Planting density	Seedling planted at different densities to determine optimum density for seedling survival and growth.	Density
Species composition	Compared survival and growth of different tree species to determine suitability of species for restoration.	Sp.
Habitat	Compared survival and growth of seedlings in different types of degraded habitat.	Habitat
Mechanical V's Manual planting	Compared survival and growth of seedlings planted by hand or using mechanized planting methods.	MecVman
Planting seedlings V's seeds V's cuttings	Compared survival and growth when using seedlings propagated in nurseries, planting seeds into ground or planting cuttings, clipped off parent trees in old-growth forest.	SeedVcut
+/- Fertilizer	Compared survival and growth of seedlings that had or had not received fertilizer.	+/-Fert
Level of fertilization	Compared survival and growth of seedlings under different concentrations of fertilizer.	Fertconc
+/- Cutting	Compared survival and growth of seedlings that had or had not had invasive grasses, shrubs or vines cut	+/-cut
Cutting frequency	Compared survival and growth following cutting at different frequencies (monthly V's quarterly).	Cutfreq
Cutting intensity	Compared survival and growth following cutting at different intensities (cutting 1m radius around seedling V's cutting entire planting area).	Cutarea

The data were strongly skewed towards smaller sized restoration projects with a median projects size of 2 ha, mean of 142 ha (Figure 7a), and 44% (n=21) of studies being conducted in projects of ≤1ha in size. Within each study the total area sampled was also small, with a median of 0.5 ha and a mean of 2.5 ha sampled (± 1.1, Figure 7b). The mean plot size used in studies again was small at 0.1ha. This could suggest some limitations of the current restoration research, as it has been show that small plot sizes lead to greater variation in estimates of AGB (Chave et al., 2003). However, this effect may be more important in old-growth forest stands that have natural landscape scale heterogeneity. In restoration areas that are planted at regular intervals, this may not be so problematic during the few years after planting

The duration of restoration projects was also skewed towards short-term studies, with a median age of 4.8 years and a mean of 6.2 years (± 1.5, Figure 7c). Just 23% (n=11) of studies were undertaken in areas that had been restored for >10 years (Table 11). The lack of long-term studies presumably reflects the relative novelty of tropical restoration ecology as a subject for research and the introduction of carbon offsetting schemes such as REDD+ since 2005 (Angelsen, 2009). It is likely that the rate of carbon sequestration will change over time, as is the case during secondary succession. Higher rates of carbon sequestration would be expected initially during early rapid growth phases and slower rates of carbon sequestration expected during later stages of growth where recruitment is balanced by mortality (Lamb, 2010). However, these trends cannot be identified in short-term projects. This means that the long-term carbon sequestration dynamics of restored forest are still unknown. This is an important gap in restoration research that seriously hinders our ability to estimate the climate change mitigation potential of forest restoration. Additionally, it is possible that recovery within restored forest could become arrested beyond the first ten years if areas are not properly managed. For example, if invasive grasses and shrubs are not kept under control they can persist in areas for many years limiting the growth of seedlings that have been planted or are naturally regenerating. Therefore focusing on the first few years of seedling establishment may not give accurate information as to the long-term impacts of restoration.

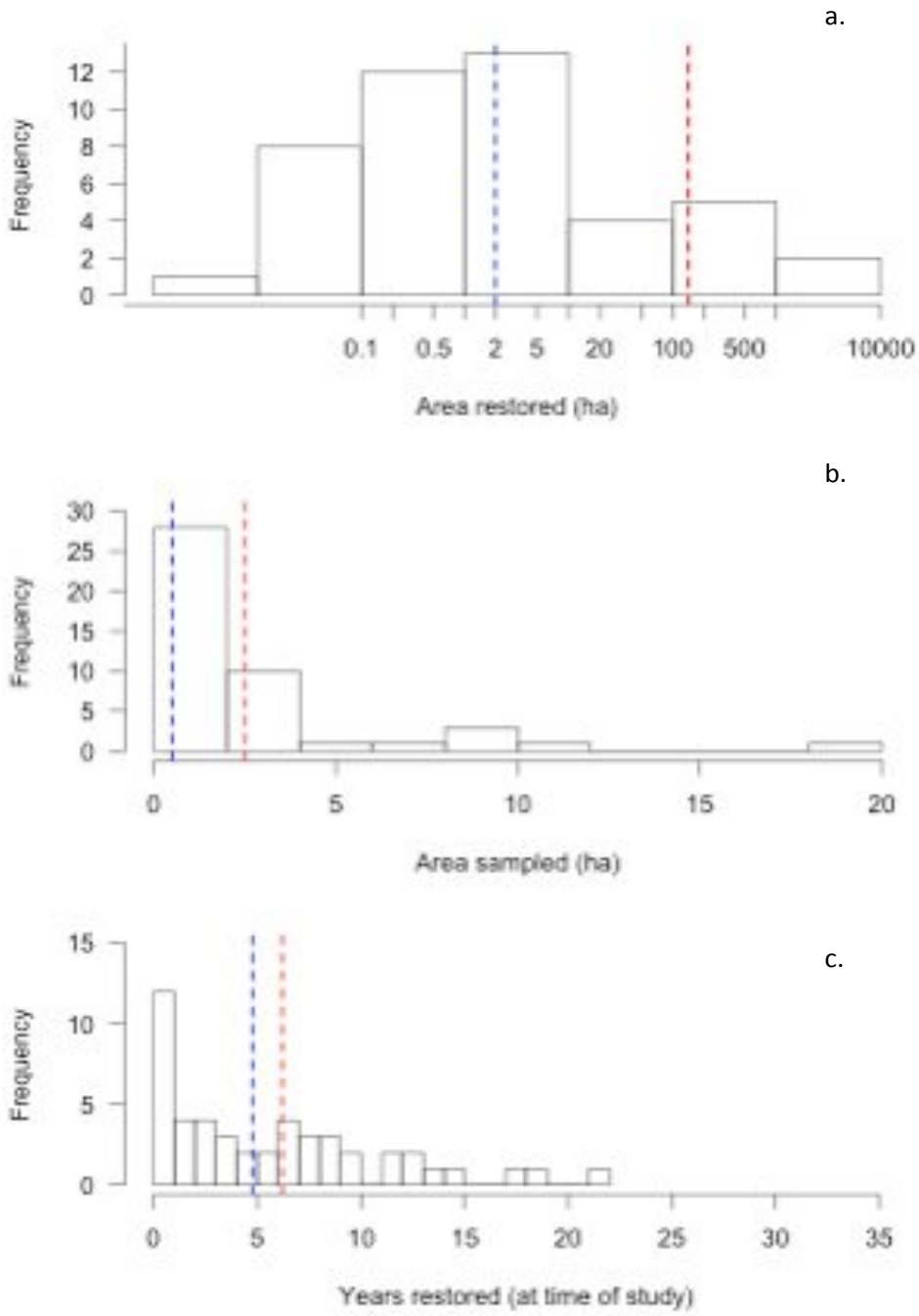

Figure 7. Frequency distribution showing a) total area (ha) of restoration projects, b) total area (ha) sampled for studies and c) number of years an area had been restored at the time of sampling, for restoration studies presented in Table 11, Red line shows mean and blue line shows median.

Numerous different restoration treatments were employed in different studies including; testing the use of fertilisers, comparing the planting of seedlings verses planting of seeds and comparing different tending regimes (see Table 12. for description of different restoration techniques). The overall aim of studies was very similar; to monitor the growth and survival of seedlings following planting to determine the most appropriate species or methods for restoration. This was predominantly done by measuring structural attributes of seedlings such as DBH, height or basal area as a response variable (n=39). Very few studies measure AGB (n=5) or diversity (n=6) as a response variable. Additionally, few studies (n=11) monitored natural regeneration within restored areas, which suggests that the biodiversity benefits of forest restoration are not well quantified.

Among the studies there was a lack of formal controls, with 62% (n=30) of studies not using controls. Of the 18 studies that did have a control, seven were comparing actively restored sites to unplanted controls that were naturally regenerating. The remaining 11 studies compared growth or survival of planted seedlings with and without an intervention. For example, the growth and survival was compared between seedling that had or had not received fertilizer (E.g. Nunez-Cruz and Bonfil, 2013)

Overall, the majority of studies compared the growth and survival of seedlings, over a small spatial scale, measuring seedling structure as a response variable (n=25), these studies were generally conducted over short time periods with the focus of research being in Latin America. Generally there is a lack of research in long-term restoration projects that have been planted over a large area and have been well sampled. Just 11 studies were conducted in restoration projects of >10 years old, seven studies were conducted in 'large' restoration projects of >50 ha, and 20 studies sampled an area or >1 ha. These studies were predominantly conducted in Brazil, Australia, and Central America (Panama, Costa Rica and Mexico).

When these three factors are combined (Studies >10 years, that sampled >1 ha, in projects of >50 ha) just two studies remain. The first is a study by Omeja et al. (2011a), conducted in Kibale National Park, Uganda, in the same restoration project where I conducted fieldwork. The data they collected for this study I have reanalysed and presented in this thesis (see Chapter 3.). The second study is by Kanowski et al. (2003), conducted in Australia using a chronosequence of restoration sites which had been planted for between

6 and 22 years. Restoration sites were compared to intact forest, monoculture plantations and unplanted areas that were naturally regenerating. In this study the structural attributes of the different habitat types were compared however the total AGB or rate of AGB accumulation in restoration site was not calculated. These findings reveal the lack of understanding about the long-term rate of AGB accumulation and biodiversity change in ecologically restored tropical forest.

This review demonstrates that there is a lack of empirical evidence showing the rate of carbon sequestration and biodiversity gains in ecologically restored tropical regions. The focus of research to data has been to determine appropriate species or methods for ecological restoration. Whilst this type of research is vital for understanding how to successfully perform ecological restoration, it could be viewed as part of precursor studies to restoration work. Given that accruing carbon credits will be the mechanism for financing restoration projects in the future under REDD+ schemes, the lack of data estimating the rate of carbon sequestration within restoration projects could seriously hinder the uptake of forest restoration work. This is an important gap in the current research that must be addressed so a strong case for enrichment planting as a successful restoration option can be made. Without knowledge of carbon sequestration, it is likely that the uptake of enrichment planting will remain low, as its carbon offsetting potential is not proven.

1.6.5. Expanding forest cover summary

All of these different restoration options have different associated carbon and biodiversity benefits summarised in Table 9 and visualised in Figure 8. For some of these options the carbon and biodiversity benefits are well understood, for example, the growth rates of different timber species planted in monoculture plantations is well documented (E.g. Onrizal, 2009). However, for other restoration options the carbon and biodiversity benefits are more uncertain and complex. The largest uncertainties are associated with the recovery rate following natural regeneration, assisted natural regeneration and enrichment planting. Fully understanding the rate of carbon sequestration and biodiversity change following forest restoration is highly complex and still involves a great deal of uncertainty. Firstly, this is because tropical lands can be degraded in a number of different ways, and can have very different climatic and edaphic conditions (see section 1.2.2.). Secondly, different areas can be affected by arrested succession to different degrees, for example, in some areas succession may just be slowed due to poor seed inputs whereas other areas may have succession halted altogether due to repeated fire or highly invasive species. Finally, different areas could receive one of many different restoration options which would result in different recovery trajectories. The combination of these three factors means that the rate of forest recovery following restoration is highly complex and difficult to predict.

Despite this complexity it is clear that certain type of restoration activity are more suitable for certain types of degraded land. It is likely that for each type of degraded land there would be an associated restoration method that would be most appropriated. For example, it is unlikely that highly degraded cattle pasture would be suitable for enrichment planting, as it would be extremely costly and high risk, as seedlings may not survive well in the open conditions. Far more appropriate would be the planting of monoculture or polyculture plantations of exotic species that are adapted to the open conditions and grow rapidly. Conversely, enrichment planting may be most effective in areas of degraded forest that still has some tree cover such as selectively logged areas or abandoned agricultural fallows. In areas like this enrichment planting would only be needed to supplement the tree cover already presents with desirable species as opposed to planting an entirely new forest. Overall it is clear that restoration is a trade off between

the suitability of land, the desired outcomes of stakeholders and the availability of funds. However successful restoration of degraded lands should be possible if sufficient planning and monitoring is undertaken.

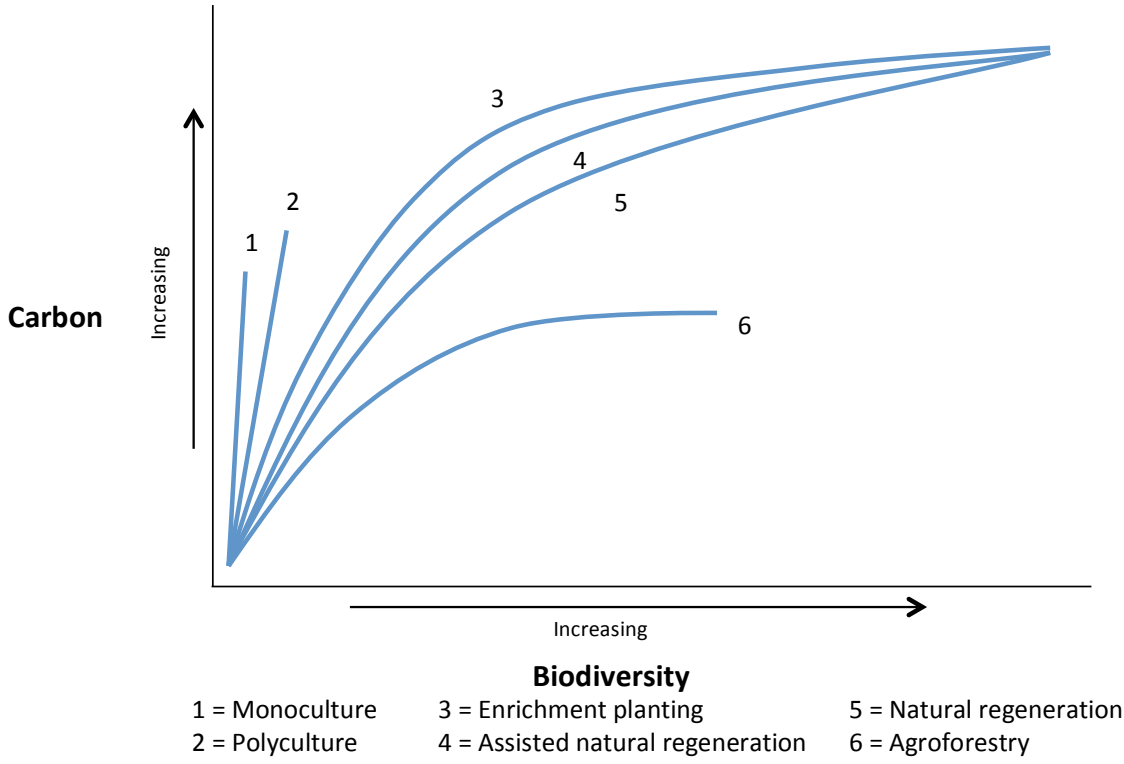

Figure 8. Conceptual diagram showing the carbon and biodiversity benefits for six different restoration options and the associated costs. Moving along each line shows how carbon and biodiversity change through time.

1.7. Large-scale restoration options

In the preceding section (section 1.6.) The carbon and biodiversity benefits associated with different restoration options were discussed and the current state of restoration research at a project scale was reviewed. However the full benefits of forest restoration come from the possibility of large-scale restoration, which could sequester large quantities of carbon if conducted over a large spatial scale and could help safeguard biodiversity if restoration efforts increase habitat connectivity of fragmented forests.

One proposed mechanism for scaling up restoration to a large spatial scale is the concept of forest landscape restoration (FLR, Laestadius et al., 2015). FLR moves forest restoration away from a small-scale site based approach, towards a large-scale integrated landscape approach, which incorporates multiple land uses in order to enhance carbon stocks, promote sustainable development, improve ecosystem function and improve the livelihoods of forest peoples (Chazdon et al., 2015, IUCN and WRI, 2014). By considering restoration across the entire landscape and integrating different forms of restoration including: ecological restoration, natural regeneration, timber plantations and agroforestry systems, you are able to get the full suite of ecosystem services from the landscape. With ecological restoration and natural regenerating enhancing regulating services such as biodiversity protection and nutrient cycling (Edwards *et al*., 2009), whilst timber plantations and agroforestry systems enhance provisioning services, providing timber and food crops (Albrecht & Kandji, 2003). And whilst different restoration options will offer different carbon sequestration benefits, by promoting wide-scale natural regeneration alongside increasing tree cover in agricultural landscapes, FLR could provide large carbon sequestration potential.

A recent map produced by the World Resource Institute (WRI) and the International Union for the Conservation of Nature (IUCN), estimated that there are approximately 2 billion ha of land are available for restoration globally, with about 1.5 billion ha suitable for 'mosaic' style restoration, and 0.5 billion ha available of 'wide-scale' restoration (IUNC and WRI, 2014). In this context mosaic restoration refers to restoration options that integrate multiple land uses including naturally regenerating forests and tree based agricultural systems, in areas that have a moderate population density (10 - 100 people

ha^{-1}), whilst wide-scale restoration refers to restoration of degraded lands back to an intact forest state, that would be predominantly in areas with low population density (<10 people ha^{-1})(Minnemeyer et al., 2011). If such large areas of land are available for restoration and the political will to enable restoration across such a large area exists then FLR could potentially offer considerable carbon sequestration benefits, which could help mitigate the effects for climate change.

Large-scale forest restoration could be of particular benefit for biodiversity conservation if done in a way that increases connectivity between forest fragments, allowing for the movement of species throughout the landscape. High rate of deforestation and forest degradation in the tropics (see section 1.4.1.) often means that old-growth tropical forest within protected areas is relied upon to conserve biodiversity. However, protected areas (PAs) are becoming increasingly isolated due to degradation between PAs. This can limit the dispersal of species across the landscape creating isolated sub-populations (Proctor et al., 2011). Resulting in some PAs failing to protect or maintain viable populations of forest species (Laurance et al., 2012). Targeted large-scale restoration to increase connectivity between forests or to create buffer zones around smaller forest fragments could help improve the dispersal of species across the landscape and prevent populations of a species becoming isolated from one another (Lamb, 2010). This is particularly important to allow species to respond to climate change, as species may have to shift their home range to find suitable habitat.

Whilst large tracts of tropical forest still remain in places such as the Amazon and Congo basin, tropical forest increasingly exists as forest fragments within an agricultural or disturbed forest matrix. Many of these areas still hold high biodiversity values but are still experiencing high rates of loss, for example the Brazilian Atlantic forest, West African forest and Sunderland biodiversity hotspots of Myers et al. (2000). Because of this PAs are increasingly being relied upon to protect biodiversity in remaining forest fragments. However, evidence has shown that PAs are failing to fully protect biodiversity. A study by Laurance et al. (2012) assessed the health of 60 PAs from across the tropics. They found that the presence of a PA in itself did not guarantee biodiversity protection, as the surrounding landscape was also important in determining PA health. They found that changes in the surrounding landscape such as reduced forest cover, increased logging and increased fire led to reductions in biodiversity, which they put down to increasing

isolation of PAs and edge effects. Consequently restoring lands surrounding forest fragments could help conserve biodiversity by increasing connectivity and decreasing edge effects.

It has been suggested that when restoring tropical forest for biodiversity conservation the most important consideration is not how much land to restore, but where restoration efforts should be focused and how restoration should be done (Lamb, 2010). Indeed trying to determine the area of land that requires restoration, in order to conserve a particular suite of species, is a complicated task. The theory of island biogeography conceived by MacArthur and Wilson (MacArthur and Wilson, 1967), demonstrated a species area relationship, showing that larger areas should contain a greater number of species, this would therefore suggest that a larger restored area would help conserve a greater number of species. However, this theory also showed that the greater the distance of an island (or in this case a forest fragment) from the mainland (or in this case area of contiguous tropical forest), the fewer species that areas would support (MacArthur and Wilson, 1967). From this theory we could therefore predict that restoring a large area that is very isolated from old-growth forest would conserve fewer species than restoring a smaller area adjacent to old-growth forest. Consequently, when restoring forest for biodiversity conservation, selecting appropriate areas is highly important.

A study by Lamb (2010) suggested that when restoring forest for biodiversity conservation there are two main approaches that would be most successful. Firstly, restoring areas around existing forest fragments to create buffer zones. He proposed that forest fragments should be prioritised based on; fragment size, fragment location, risk of logging or removal and the species contained within a fragment, suggesting that more recently fragmented forest that still has high species richness, should be given higher priority than old forest fragments that are likely to represent a depauperate community as a result of local extinctions.

Evidence suggests that species area relationships (SARs) exist in forest fragments. A review by Hill et al. (2011) investigated SARs across the tropics for birds in 26 studies. They found that 50% of studies had significant SARs, with smaller fragments having lower species richness. Within the same study they also assessed SARs of insects (ants, moths and butterflies) within forest fragments in Borneo and found significant SARs for each

taxa. Additionally, forest fragments experience edge effects that have been seen to reduce abundance of species such as understory birds, butterflies and ants and alter tree species composition, due to increased wind-throw and desiccation, causing increased mortality (Laurance et al., 2011). The problems associated with edge effects are more noticeable in small fragments as they are proportionally more influenced by edge effects than large forest fragments. Therefore restoring areas of degraded or deforested land surrounding forest fragments creating buffers could be an effective means of conserving biodiversity by increasing fragment size and reducing the effects of edge.

The second suggestion by Lamb (2010) for combining forest restoration with biodiversity conservation is to restore areas between forest fragments to increase connectivity across the landscape, thereby creating corridors for species dispersal. There is some evidence to suggest that current networks of old-growth forest fragments and PAs are not sufficiently well connected to allow for dispersal of species. For example, a study by Proctor et al. (2011) assessed connectivity of remaining forest across the island of Borneo, and examined how well current PAs protected highly connected forest. They found that 64% of highly connected forest and 50% of PAs occurred at elevations >400 m, where ~25% of land area is found, whereas just 15% of highly connected forest and 38% of PAs were found <200 m, where >60% of total lands area and 43% of forest area is located. They concluded that currently high altitude forest in the centre of Borneo is well connected and well represented by PAs. However, low altitude forest, which covers a large proportion of the land areas, is currently poorly connected and, proportional to land area is poorly represented by PAs, meaning that low altitude forest could be vulnerable to further degradation. The poor connectivity between existing old-growth forests is clearly problematic for biodiversity as populations within poorly connected and fragmented forests have and increased rick of inbreeding (Benedick et al., 2007) and are more vulnerable to stochastic extinction events such as fire (Lande, 1993). Therefore large-scale forest restoration to form corridors between existing forest fragments could be an effective means of conserving biodiversity. This could help reduce genetic isolation of populations and allow for the dispersal of species across the landscape.

Improving the dispersal ability of species is important in two many ways. Firstly, it is important for species that have a large home range such as large mammals, who come into increasing contact with human in fragmented landscapes, resulting in higher hunting

pressure (Woodroffe and Ginsberg, 1998), and for forest specialist or endemic species that naturally have a low population density and are unable to cross agricultural or disturbed areas (Laurance et al., 2002). Secondly, improving dispersal is important for helping species adapt to climate change, enabling them to shift there distributions and move into more suitable habitat (Hodgson et al., 2009). Evidence has shown that species have shifted their ranges in response to climate change. A meta-analysis by Chen et al. (2011b) which assessed range shifts in response to climate change in 23 taxa, estimated the distribution of species had shifted to higher latitudes at a rate of 16.9 km decade^{-1} and shifted to higher elevations at a rate of 11 m uphill decade^{-1}. However, this meta-analysis included studies from both temperate and tropical regions. When focusing specifically on tropical regions similar shifts have been observed. A study by Chen et al. (2011a) assessed range shift in moths on Mount Kinabalu in Borneo over a 42 year period. Over this period the area experienced a 0.7 ˚C increase in temperature. They estimated rages shifts of between 52 and 68 m uphill. Studies such as these suggest that species are shifting their ranges in response to changing climate therefore, increasing habitat connectivity will be important to enable this to happen, meaning that forest restoration over a large scale could be an important climate change adaption strategy.

While it is certain that old-growth tropical forest is unrivalled in its biodiversity, large-scale restoration of areas to increase connectivity and allow for species dispersal is essential to reverse past losses of biodiversity, particularly in the face of climate change to allow for species range shifts. Therefore, restoration of tropical forest has a unique dual benefit in that, it can help forest ecosystem become more resilient to climate change, whilst also helping to mitigate the effects of climate change through sequestration of carbon. However, in order for large-scale restoration to be achieved and these goals to be reached will require strong governance, international policies and co-operation of local communities.

1.8. Policy Frameworks

1.8.1. Climate Change Policy

Restoration of forests to mitigate the effect of climate change has climbed in international political agenda in recent years, culminating in the signing of the Paris agreement in 2015. The Paris agreement state an ambition to keep global temperatures well below 2˚C above pre-industrial levels, and achieve net zero greenhouse gas emissions (GHG) by the second half of this century (UNFCCC, 2015). Additionally it states that parties should strive to conserve and enhance sinks of GHGs, specifically referencing the use of forests, and activities for reducing emission from deforestation and forest degradation (REDD+). In addition to the Paris agreement large scale policy initiative are setting ambitions global restoration target, these include the BONN challenge, which aims to restore 150 million ha of forest by 2020 (The BONN Challenge, 2016) and the New York Declaration on Forest, which builds on the BONN challenge and aims to restore an additional 200 million ha by 2030 (UNFCCC, 2014). Further initiatives are also promoting restoration in tropical regions such as the WRI Initiative 20 x 20, which aims to restore 20 million ha by 2020 across Latin America (WRI, 2015b), and WRI AFR100 which aims to restore 100 million ha by 2030 (WRI, 2015a). Such ambitious targets for forest restoration show a general acceptance of the importance of forest restoration for increasing terrestrial carbon storage to help offset the effect of climate change (Aronson and Alexander, 2013)

1.8.1.1.Reducing Emissions from Deforestation and forest Degradation (REDD+)

With the inclusion of REDD+ in the Paris agreement it is likely that this will be the predominant mechanism for financing restoration activities. REDD+ was first proposed to the UNFCCC in 2005, by Costa Rica and Papua New Guinea, on behalf of the Coalition for Rainforest Nations (CfRN), and has subsequently been the subject of much debate and negotiation (IPCC, 2014). REDD+ is a voluntary carbon payments scheme, whereby developing countries can undertake forest related activities to mitigate the effects of climate change. These activities include; avoided deforestation and avoided forest degradation, sustainable management of forest carbon stocks, for example reduced impact logging to retain more carbon on forest land after logging, and finally enhancement of carbon stocks via enrichment planting or ANR activities (Parker and Trivedi, 2009).

The REDD+ framework has a broad national approach, as opposed to the project-based approach. This allows developing countries to introduce national policies the promote REDD+ activities, with the hope that this will produce larger carbon emissions reductions than individual projects (IPCC, 2014). Payments for emissions reductions under REDD+ are results-based, with verified carbon outcomes receiving payments after they are achieved as opposed to projects being financed from the outset (IPCC, 2014). REDD+ is often presented as a 'win win' climate change mitigation solution, as it offers a number of co-benefits alongside climate change mitigation including; economic benefits for developing countries, social and livelihood benefits for indigenous and local people and ecosystem service co-benefits such as biodiversity protection, watershed protection and soil protection amongst others (Angelsen, 2008, Visseren-Hamakers et al., 2012).

However, prior to REDD+ being implemented a number of issues need to be resolved, this includes issues related to the effectiveness of carbon sequestration generally, and issues related specifically to the implementation of REDD+. Issues related to carbon sequestration as a concept include; non-permanence, saturation, leakage, additionality and the impacts of climate change (IPCC, 2014). Non-permanence is the potential re-release of sequestered carbon. This can be accidental, for example, as a result of a natural disaster such as fire, or intentional. There are some types of carbon sequestration project that are predisposed to non-permanence, such as afforestation of monoculture plantations that are likely to be cut down for timber (Angelsen, 2008). However non-permanence could be related to possible future changes in government policy that could open areas up to logging once more. To resolve this issue long term governance and protection of carbon sequestration projects is needed to ensure long-term emission reductions (Angelsen, 2008).

Leakage occurs when a carbon reducing activity in one location leads to an increase in emissions elsewhere meaning that net emissions are not reduced (IPCC, 2014). Leakage has been recognised as one of the biggest challenges for REDD+, and there is much debate over the scale (regional, national, sub-national) at which it should be measured (Atmadja and Verchot, 2012). For both the issues of non-permanence and leakage it is hoped that the national based approach of REDD+ will help reduce some of the potential problems, with a centralized system allowing for greater co-ordination and standardisation, making

it easier to monitor at a national scale (Atmadja and Verchot, 2012, Oestreicher et al., 2009). However it has been suggested that this will threaten to recentralise governance of forests, reducing access to land and removing land rights of indigenous and local people (Phelps et al., 2010)

Another issue for carbon sequestration projects that needs to be considered is the concept of additionality. For accurate carbon accounting it is important to determine if carbon is sequestered as a result of project activities, or if carbon would have been sequestered anyway without project activities. For this to be calculated accurate baseline carbon values must be estimated prior to projects commencing, so that additional carbon sequestered as a result of project activities can be estimated, however, currently there is no agreed method for calculating baselines making this difficult (Angelsen, 2008). Carbon sequestration within forests is finite with different forest types having different natural maximum carbon storage value (Pan et al., 2011), this is when a forest becomes saturated and the sink strength of forests is reduced. The naturally higher carbon density of tropical forests means they offer greater carbon sequestration than other forest types. Finally, the resilience of forest ecosystems to future climate change is important in determining the success of carbon sequestration projects. It is likely that future climate change will lead to more extreme weather, events such as drought, potentially increasing the risk of fire. (Bonan, 2008). The ability of ecosystems to withstand such events will be important in determining long-term carbon sequestration and the overall success of REDD+ projects.

For the successful implementation of REDD+, and to address some of the issues mentioned above, accurate monitoring, reporting and verification (MRV) of changes in forest carbon emissions and stocks against baseline emissions scenarios is required. Without accurate MRV, payments for carbon enhancement and emissions reductions cannot be made. Within the REDD+ framework MRV is to be undertaken at a national level, with individual countries measuring changes in forest area and changes in carbon stocks (Angelsen, 2009), in line with IPCC good practice guidelines (IPCC, 2006a). The use of remote sensing technology is likely to be the most practical method for undertaking MRV at a national scale. The advent of new technologies such as radar and LiDAR will make measuring biomass stocks of forest over a large area possible (Mitchard et al., 2012). Despite MRV occurring at a national level, consistency among countries is required and methods to

scale down MRV at a project scale is needed to estimate actual on the ground carbon emissions (Angelsen, 2009).

1.8.2. Biodiversity policy

Following increasing recognition of the importance of the earth's biodiversity for human wellbeing and a need to conserve it for future generations the United Nations Environment Programme (UNEP), established the Convention on Biological Diversity (CBD). The CBD is an international treaty, which has the aim of conserving biodiversity and promoting its sustainable use and legally binds countries to implements strategies to meet these aims. Following the UNs International year of biodiversity in 2010 the CBD adopted a new strategic plan, which included the Aichi biodiversity targets (CBD, 2013, CBD, 2011). The Aichi biodiversity targets are 20 targets to help kerb biodiversity loss, enhance the benefits gained from biodiversity, safeguard ecosystem and genetic diversity and increase awareness of issues related to biodiversity. These targets are separated under five main goals to be implemented by 2020.

Of these 20 targets, four are of particular relevance to forestry, relating to reducing forest loss and restoring forest ecosystems to enhance biodiversity and therefore are very complimentary to REDD+ objectives (Figure 9. Miles et al., 2012). These four targets are: Target 5 – to halve or reduce habitat loss by 2020 and to reduce degradation and habitat fragmentation. Whilst this target covers all natural habitats it specifically identifies forests and their importance for biodiversity conservation, and therefore is directly related to the primary aim of REDD+ to reduce deforestation and forest degradation. Target 7 relates to sustainable management of agricultural and forest areas to ensure biodiversity conservation. Sustainable management of forest, for example by employing reduced impact logging techniques, can have multiple benefits of; minimising the loss of biomass following logging thereby enhancing carbon storage, minimising biodiversity loss following logging and improving sustainable production of forest products including timber and NTFPs.

Target 11 calls for expansion of protected areas, particularly in areas of high biodiversity value to improve the connectivity of ecosystems across the landscape and to improve management of protected areas. Enhancing the area of protected areas and connecting

fragmented areas via corridors has clear benefits for biodiversity conservation. Expanding protected areas can help safeguard carbon stocks in areas that may otherwise be cleared of forest cover, however, without effective management carbon losses can still occur as a result of illegal activities, therefore enhancing the management of protected areas can help prevent this. Finally target 15 states that 15% of degraded ecosystems should be restored by 2020, to enhance carbon stocks, create more resilient ecosystems and enhance biodiversity thereby contributing to climate change mitigation. This is the only Aichi target to explicitly state the importance of ecosystems in climate regulation via carbon storage and sequestration and therefore is directly linked to the goals of REDD+ (Miles et al., 2012). Furthermore, target 15 highlights the importance of resilient and biodiverse ecosystems in maintaining carbon stocks into the future.

Further to this, the UN-REDD programme has noted that these four targets are directly related to REDD+ activities in helping to meet two REDD+ safeguards. Firstly, that REDD+ activities are consistent with relevant international conventions, which includes the CBD. Secondly, that REDD+ activities help conserve natural forest and biodiversity and incentivise conservation of forests and the ecosystem services they provide (UNFCCC, 2010). Through the Aichi biodiversity targets the CBD has set clear, legally binding goals to enhance biodiversity within forests, reduce forest loss, increase forest restoration and increase carbon storage and therefore these targets are directly related to the aims of REDD+. Furthermore, both the Aichi biodiversity targets and the REDD+ safeguards clearly emphasise the importance of natural forest cover in creating climate resilient ecosystems that enhance biodiversity and store carbon. With these two international policy initiatives promoting the benefits of forest restoration for reducing carbon emissions and reducing biodiversity loss it is clear that research showing the effects of forest restoration is needed.

Goal A: Reduce the direct pressures on biodiversity and promote sustainable use

HABITAT LOSS HALVED OR REDUCED

Rate of habitat loss halved in all habitats, including forests
Degradation and fragmentation significantly reduced

SUSTAINABLE AGRIGULTURE, AQUACULTURE AND FORESTRY

Sustainable management of areas under agriculture, aquaculture and forestry, ensuring conservation of biodiversity

Goal C: To improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity

PROTECTED AREAS INCREASED AND IMPROVED

17% of terrestrial and inland water areas conserved and managed, especially areas of importance biodiversity and ecosystem services
Create ecologically representative and well connected systems of protected areas

Goal D: Enhance the benefits to all from biodiversity and ecosystem services

ECOSYSTEMS RESTORED AND RESILIANCE ENHANCED

Contribution of biodiversity to carbon stocks enhanced, through conservation and restoration
Restoration of 15% of degraded ecosystems, contributing to climate change mitigation

Figure 9. Description of the four main Aichi Biodiversity targets related to forestry.

1.9. Aims and Objectives

This literature review has pointed out the complex nature of deforestation and forest degradation in the tropics, and how they contribute to carbon emissions, biodiversity losses and depletion of ecosystem services. I have explained how large-scale abandonment of deforested and degraded lands could allow for the expansion of forest cover, which could in turn, increase terrestrial carbon storage, improve biodiversity and regain ecosystem services. However, there is a lack of evidence quantifying the rate for forest recovery following the abandonment of deforested and degraded lands. As well as a lack of understanding about the climate change benefits of forest restoration over a large spatial scale. This PhD project aims to address some of these gaps.

1.9.1. Aims

This thesis aims to

1) Quantify the relationship between the type and severity of forest degradation and the rate of ecosystem recovery, and determine how forest restoration could modify recovery.

2) Improve understanding of carbon sequestration and tree diversity change within restored tropical forest, at two established long-term forest restoration projects

3) Quantify the carbon sequestration potential of tropical forest restoration over large spatial scales.

1.9.2. Objectives

Objective 1: Quantify the rate of natural regeneration in forests recovering after different types of disturbance

1.1 Conduct a systematic review of literature monitoring change in carbon storage over time, in forest recovering following disturbance

1.2 Assess the effects of land use type (type of disturbance) on the rate of carbon sequestration

1.3 Assess how climate affects the rate of carbon sequestration,

Objective 2: Estimate the rate of forest recovery in actively restored tropical forest

2.1 Conduct fieldwork in two long-term restoration projects with different disturbance histories.

2.2 Estimate the rate of forest recovery, in terms of change in aboveground biomass, basal area, wood density and stem density.

2.3 Estimate the effect of forest restoration on tree diversity

Objective 3: Estimate the total carbon storage potential of landscape scale restoration over a 100 year timeframe

3.1 Estimate the time averaged carbon storage per ha in different land use options available for landscape scale restoration, over a 100 year time period

3.2 Quantify the net carbon benefit of different landscape scale restoration options over one million ha, under different land use scenarios.

2. Methods

To tackle the objectives of this thesis, analysis was divided into three sections split into four research chapters. Firstly, I undertook a systematic review of literature to determine the effects of type of forest degradation on the rate of forest recovery (chapter 2). I then conducted fieldwork in two actively restored tropical forest restoration projects, which had different land use histories to estimate carbon sequestration rates and changes in tree diversity resulting from restoration (chapter 4 and chapter 5). Finally, I quantified the carbon sequestration potential of large-scale tropical forest restoration, by modelling long-term (100 year) carbon sequestration of different forest restoration options. The general methods used in this thesis are described in this chapter.

2.1. Chapter 3

To quantify the rate of natural regeneration in forests recovering after different types of disturbance (objective one), I undertook a systematic review of literature, and for all suitable studies found, data were entered into a database and analysed. A systematic review was conducted to find literature which assessed AGB recovery in forest naturally regenerating following disturbance, using the protocol described in Pullin and Stewart (2006), which follows five key steps: 1) define research question, 2) determine inclusion criteria for studies *a priori*, 3) decide search criteria that balances sensitivity (getting all relevant information) and specificity (the proportion of relevant hits), 4) extract relevant papers from search first by title and then by abstract, and 5) input all extracted data into database for analysis.

For each site found I extracted data on: land use type; original forest type; methods used (chronosequence or repeat measurements); plot size (ha), number of plots measured, minimum DBH cut-off (cm); latitude; longitude; duration of land use prior to recovery. Within each site the AGB (Mg ha^{-1}) and age (i.e. number of years recovery, since agricultural or logging activities were terminated) of forest plots was recorded. In some sites, AGB values were the mean of multiple plots, rather than a single AGB value taken from one plot. Site latitude and longitude were used to extract mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm) and precipitation in the driest quarter (DRYQ, mm) at a 1 km resolution from the WorldClim dataset (Hijmans et al., 2005). For

one island site (Ruiz et al., 2005), climate data was unavailable, therefore in analysis which included climate data, this site was exclude.

Data were analysed using linear mixed-effects modelling to determine if the type of degradation (pasture, permanent agriculture, shifting cultivation or selective logging) affected the rate of AGB accumulation. Or, if the rate of AGB accumulation was determined by other climatic (MAP, MAT or DRYQ) or biogeographic (region) variables. Mixed-effects modelling was suitable for analysis as it allows both continuous and categorical fixed effects to be included in models alongside random effects (Crawley, 2012). Random effects needed to be included in analysis to account for the hierarchical structure of data collected at different spatial scales (i.e. plots data within different sites, and site data at different locations). For full details of data analysis see chapter 3.

2.2. Chapters 4 and 5

To address objective two of this thesis I undertook fieldwork in two actively restored tropical forest restoration projects, in Kibale National Park, Uganda and in Sabah, Malaysian Borneo. Both of these sites had undergone active forest restoration, in the form of replanting with native species and cutting of grasses, shrubs and vines, following degradation. In Uganda, the original forest had undergone agricultural encroachment and was dominated by elephant grass (*Pennisetum purpureum*) when restoration began in 1992. In Borneo, the forest was selectively logged in 1989, and restored in 1999. For detailed site information see section 4.3 (Uganda) and section 5.3 (Borneo).

To assess changes in AGB, forest structure and tree diversity over time permanent sample plot (PSP) networks were used. In PSPs the same individuals are measured over multiple census periods, this method gives greater accuracy when assessing temporal changes in AGB compared to forest chronosequences, which used a space for time substitution (Bakker et al., 1996, Condit, 1998). Therefore, changes observed in forest chronosequence studies may be due to variation in site conditions among plots (e.g. soils or topography) rather than solely due to site age. Furthermore, using PSPs means aboveground wood productivity, recruitment and mortality of individuals can be assessed (e.g. Talbot et al., 2014). In Uganda plots were established in 2005 and re-established by me in 2013,

allowing for changed to be assessed over 18 years. In Borneo plots were established in 2007, remeasured in 2010 and remeasured again in 2015 by myself.

Within plots all trees over a specified diameter at breast height (DBH, taken at 1.3m) were measured. For each individual DBH, height and species was recorded, and date was used to calculate AGB. Plot based sample design varied between sites, for full details on sample design see respective chapters.

2.2.1. Data Analysis

2.2.1.1.Biomass

Aboveground biomass, in Mg dry mass ha^{-1} (1 Mg = 1 metric ton) was calculated as:

$$AGB = 0.0673 \times (\rho D^2 H)^{0.976}$$

Where ρ = wood density (g cm^{-3}), D = DBH in cm and H = height in m (Chave et al., 2014). Wood density (WD) values for each species were obtained from the global wood density database (Zanne, 2009, Chave et al., 2006) available from the Dryad data repository (http://datadryad.org/). Where species-specific wood densities were not available, or when individuals were only identified to morpho-species, the genus mean or familial mean wood densities were used (Lewis et al. 2009). If family was unknown then the mean plot wood density was used. Carbon content was considered to be 47.1% (± 0.4%), which has been shown to be more suitable carbon value in tropical forests than the commonly used 50% (Thomas and Martin, 2012).

2.2.1.2.Tree diversity and species composition

Within community α -diversity of trees was analysed using Hill numbers, which measure diversity along a spectrum from species richness (N_0) at one end, to species evenness (N_2), at the other end (Hill, 1973). Here I used hill numbers N_0 = Species richness and N_2 = Inverse of Simpsons D which is related to species evenness. Between community β-diversity was analysed using Sørensen similarity indices, which measured the similarity in

species composition and abundance amongst different habitats. This produced a score between 0 and 1, with 0 = plots had no species in common and 1 = plots were identical. The mean similarity score of all pairwise comparisons was used to determine the similarity among habitats.

The differences in community composition between habitats at each census were analysed using Non-metric Multidimensional scaling (NMDS), calculated using the Bray-Curtis dissimilarity indices. NMDS shows graphically the similarity of different samples and species. With sample points that were close together, likely to have similar species composition and species located close to sample points having a high likelihood of being found within that sample (Lepš, 2003). The mean NMDS scores of all plots at each census interval was calculated and plotted on NMDS ordination plots to determine how species composition had changed over time. All α and β diversity and ordination analyses were done using the Vegan package (Oksanen et al., 2013) in R (R Core Team, 2013).

2.3. Chapter 6

The final objective of this thesis was to quantify total carbon sequestration within restored tropical forests over large spatial scales. This analysis involved four main stages. Firstly, I undertook a literature search to identify tree dominated land cover types that have been proposed as suitable for landscape scale restoration (FLR) in the tropics (IUCN and WRI, 2014, Arora and Montenegro, 2011, Chazdon et al., 2016b, Budiharta et al., 2014). Secondly, from these literature searches I found rates of carbon sequestration for each land use option. Thirdly, carbon sequestration was modelled over a 100-year timeframe for each land use option. Finally, total carbon sequestration over a 100-year timeframe was extrapolated over a 1 million ha (Mha) area using different land use scenarios to estimate large-scale carbon storage potential from forest restoration.

For literature searches I used an FAO definition of forest (tree cover of at least 10%, covering over 0.5ha with trees >5 m in height; FAO (2000)), which identified six possible land use options suitable for restoation. These were: 1) natural regeneration of degraded forest, 2) natural regeneration of abandoned agricultural land, 3) rotational selective logging of native forest, 4) timber plantations, 5) agroforestry systems and 6) oil palm plantations. Land uses one to three were grouped: one and two are naturally regenerating

systems recovering back towards intact forest, whilst the third, rotational logging, allows for the extraction of timber resources, but retains native forest cover and therefore was classed as a 'naturally' regenerating land use type. I defined degraded forest as forests that had undergone a reduction in aboveground biomass (AGB) and tree cover but retained native forest (GOFC-GOLD, 2015), which in this context predominantly refers to selectively logged forest. Land uses four to six were all tree based agricultural (TBA) systems that were rotational and allowed for the extraction of timber products and crops. For timber plantations I specifically focused on *Eucalyptus* and *Acacia* as these are the most common timber species in the tropics (Bouillet et al., 2013). I also compare FLR land use options to reference primary forest. See section 6.3.1 for details of serch terms and inclusion criterial for studies.

For each of these six land use options I found carbon sequestration rates and modelled them over a 100-year time horizon. A 100-year time horizon was used, as it is a long enough time period to monitor meaningful long-term carbon sequestration resulting from restoration. In addition to carbon sequestration in aboveground carbon (AGC) pools, I used published root: shoot ratios and live AGB: necromass ratios to estimate carbon storage in belowground and necromass pools for each land use. See section 6.3.1 for details on how carbon sequestration and root: shoot rations were calculated. As the Paris agreement includes commitments to cut all greenhouse gases, and not just CO_2 (UNFCCC, 2015), the N_2O emissions from fertiliser application in TBA systems were calculated and accounted for in modelling. See section 6.4.5 for a full description of N_2O calculations

2.3.1. Scenario predictions

To explore the differing impacts of different land cover schemes used to restore landscapes and improved ecological function, I simulated three different scenarios over a one Mha sample area. The first land use projection was to restore the 1 Mha back to intact forest. The second was the other extreme: convert the 1 Mha to oil palm. A middle scenario, where half the area (0.5 Mha) is restored to intact forest, and the other half restored using TBA options explores what may occur in a real-world restoration landscapes. See section 6.3.3 for full details on land use scenarios.

3. Aboveground Biomass Recovery Trajectories Following Tropical Forest Land Use Change

3.1. Abstract

Logging, agriculture and other human impacts on land tend to reduce the amount of terrestrial carbon stored. Following this disturbance, if the land is left to naturally regenerate, carbon storage tends to increase. If large areas of land were left to regenerate this could assist in reducing carbon dioxide levels in the atmosphere. The recovery trajectories of such lands may vary substantially due to the severity of the prior land use or differences in local climate. However, our understanding of the factors influencing the recovery of naturally regenerating forest is limited. I undertook a pan-tropical systematic review of aboveground biomass (AGB) recovery literature, to estimate the recovery trajectories of naturally regenerating land following shifting cultivation, permanent agriculture, pasture and selective logging. I assessed the effect of land use type, continent and climate on AGB recovery using mixed effects modelling. Land use type had no significant effect on AGB accumulation, on average adding 4.9 Mg dry mass ha^{-1} yr^{-1} over the first 20 years (100 Mg dry mass ha^{-1} after 20 years recovery), or 4.3 Mg ha^{-1} yr^{-1} over the first 40 years (171 Mg ha^{-1} after 40 years recovery). Mean annual precipitation (MAP) had a significant positive effect on AGB recovery; This observed impact of MAP on AGB accumulation could have important implications for the carbon storage potential of naturally regenerating forest if predicted changes in drought frequency related to climate change occur in the tropics. However, it is clear that AGB accumulation rates following the cessation of agriculture and logging are high. Thus there is an opportunity to increasing terrestrial carbon storage to mitigate climate change.

3.2. Introduction

Approximately 7.4 million ha yr^{-1} of tropical forest were converted to other land cover types between 2000 and 2010 (Achard et al., 2014, Hansen et al., 2013), a major determinant of the gross carbon emissions from land-use change, of between 0.9 Pg C yr^{-1} and 2.6 Pg C yr^{-1} (Grace et al., 2014, Achard et al., 2014, FAO, 2010, Pan et al., 2011). Furthermore, degradation of tropical forest, primarily from selective logging, emits an additional 0.3 Pg C yr^{-1} (Grace et al., 2014). The agricultural lands resulting from deforestation, used for crop production, cattle ranching and shifting cultivation, are often abandoned due to reductions in crop yields, the invasion of unpalatable grasses into pastures, soil degradation, and socioeconomic factors including rural to urban migration (Aide et al., 1995, Buschbacher, 1986, Benayas et al., 2007).

Such abandonment of agricultural lands, coupled with large areas of selectively logged forest, has resulted in the area of naturally regenerating forest expanding (Chazdon, 2014). The area of regrowth forest in the tropics estimated to cover 557 million ha (Pan et al., 2011), increasing by 1.6 million ha yr^{-1} (Achard et al., 2014), and sequestering 1.6 Pg C yr^{-1} (Pan et al., 2011). As such naturally regenerating forest are often seen as a low cost carbon sequestration mechanism (Houghton et al., 2015). Furthermore, it has been proposed that if naturally regenerating forest were allowed to persist and recover back to an intact forest state, over a large enough area then they could be an important climate change mitigation option (Houghton et al., 2015, Canadell and Raupach, 2008), with international policy initiatives such as REDD+ promoting natural regeneration of degraded forest to help increase terrestrial carbon storage (Birdsey et al., 2013). A recent study by Chazdon et al. (2016b) estimated carbon sequestration in neotropical secondary forest, estimating that a total of 8.5 Pg C could be sequestered, over 40 years, if all of the 2.4 million ha of neotropical secondary forest were left to naturally regenerate, demonstrating the carbon sequestration potential of naturally regenerating forests.

However, to assess the role of natural regeneration as a climate change mitigation option, we must first understand how naturally regenerating forests recover following abandonment, including the factors influencing carbon sequestration rates. However, land use change in the tropics is complex; human land uses vary considerably, including in

intensity. For example, from forest converted to cattle pasture, at the highest level of intensity, to selectively logged forest at the lowest level of intensity. Furthermore, tropical forest also exist over broad environmental gradients, with large variation in temperature, precipitation and rainfall seasonality (Malhi and Wright, 2004, Hijmans et al., 2005). Such difference in the severity of land use change and environmental conditions may result in highly variable recovery trajectories in naturally regenerating forest (Toledo et al., 2011, Chazdon, 2003). These differences in recovery trajectories will have important implications for terrestrial carbon storage and the climate change mitigation potential available from naturally regenerating forests. Therefore understanding the net change in aboveground biomass (AGB), i.e. the carbon sequestration, rate following different types of land use and in difference locations is essential to better understand the potential that forest regeneration could contribute to climate mitigation.

Many past studies have quantified net AGB change following a change in land-use in various tropical settings (e.g. Saldarriaga et al., 1988, Uhl et al., 1988, Alves et al., 1997, Hughes et al., 1999). There have also been successful syntheses of research findings (e.g. Ziegler et al., 2012, Bonner et al., 2013, Martin et al., 2015, Poorter et al., 2016). However, so far reviews have focused on a single region or one land use type. For example a recent study by Poorter et al. (2016), which focused on the Neotropics, used data from 26 studies to estimate carbon sequestration within secondary forests recovering on abandoned agricultural land. They estimated a carbon sequestration rate of 6.1 Mg ha^{-1} yr^{-1} in the first 20 years following abandonments, and predicted it would take a median of 66 years for secondary forest to recover 90% of old-growth forest values. Another study by Bonner et al. (2013) compared AGB accumulation in secondary forests recovering following agricultural use and timber plantations. They found significantly higher AGB accumulation in timber plantations compared to secondary forest at 10.9 Mg ha^{-1} yr^{-1} and 7.7 Mg ha^{-1} yr^{-1}, respectively. Yet, it is unclear if the differences between these two studies are related to prior land use, its intensity, or studies selected from differing climates.

Here I overcome these limitations by undertaking a systematic review of studies reporting net AGB change in areas naturally regenerating following abandonment, from across the tropics, to understand what factors influence recovery and how this varies in different tropical regions. Specifically, I aim to 1) determine the rate of AGB accumulation in naturally regenerating forest recovering following disturbance, and 2) determine what

factors including: land use type, biogeography and climate, influence the variation in AGB accumulation.

3.3. Methods

3.3.1. Systematic review

I undertook a systematic review of literature, which assessed AGB recovery in forest naturally regenerating following disturbance. Literature searches were carried out in the Web of Science database using the search terms: (tropic* AND forest* AND (biomass OR carbon OR agb OR recover* OR structur* OR accumulat*) AND (pasture OR slash* OR shift* cultivat* OR agricult*) AND abandon*), with literature searches looking within the title and abstract of papers. Additional references were also found in the appendices of Bonner et al. (2013), Poorter et al. (2016), and Ziegler et al. (2012). To be included in this review studies had to meet the following inclusion criteria:

1. Studies provided geolocated estimates of AGB change over time, using either forest chronosequences or repeated measurements of permanent sample plots (i.e. estimates of AGB at two points in time, so a rate of net AGB change could be calculated). Estimates using remotely sensed data only were excluded.
2. Studies were conducted in the tropics i.e. the study site lay within 23.5^{o} latitude north or south.
3. The original land cover of the study site was closed canopy tropical forest.
4. The study site had undergone a specified form of land use change and had subsequently been abandoned and left to naturally regenerate (i.e. studies monitoring AGB changes in tropical timber plantations were excluded).
5. Studies quoted the age of forest stands at time of measurement (i.e. the time since abandonment) for chronosequences, and census dates for repeat measures of permanent sample plots.

This literature search produced 529 references, 163 relevant references after reading the title and abstract, and 52 studied that conformed to the full inclusion criteria (Figure 10). If studies reported data in tables, it was extracted directly and entered into a database. If data was reported graphically, data was extracted using the programme Data Thief III (Tummers, 2006). Data from an additional 16 references were extracted from the supplementary information of Poorter et al. (2016). Metadata for each site used in analysis is shown in Appendix 1. See section 2.1 for details of data extracted from each site.

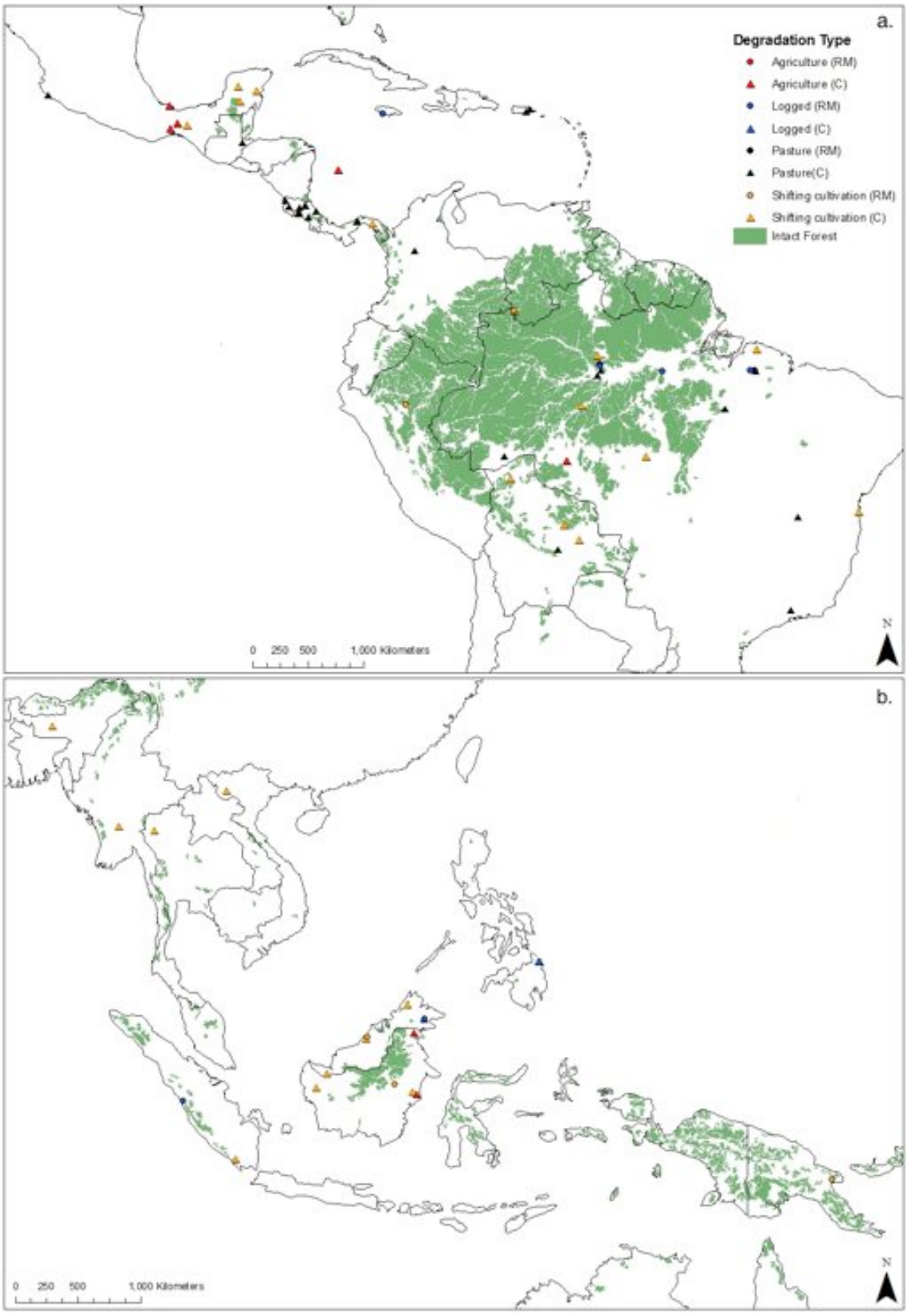

Figure 10. Map showing locations of study sites, degradation type and if studies used sronosequences of repeat smapling methods in a. south America, b. Southeast Asia and c. Africa. Green areas show intact forest areas (Source: Hansen et al. 2013, accessed through Global Forest Watch - www.globalforestwatch.org).

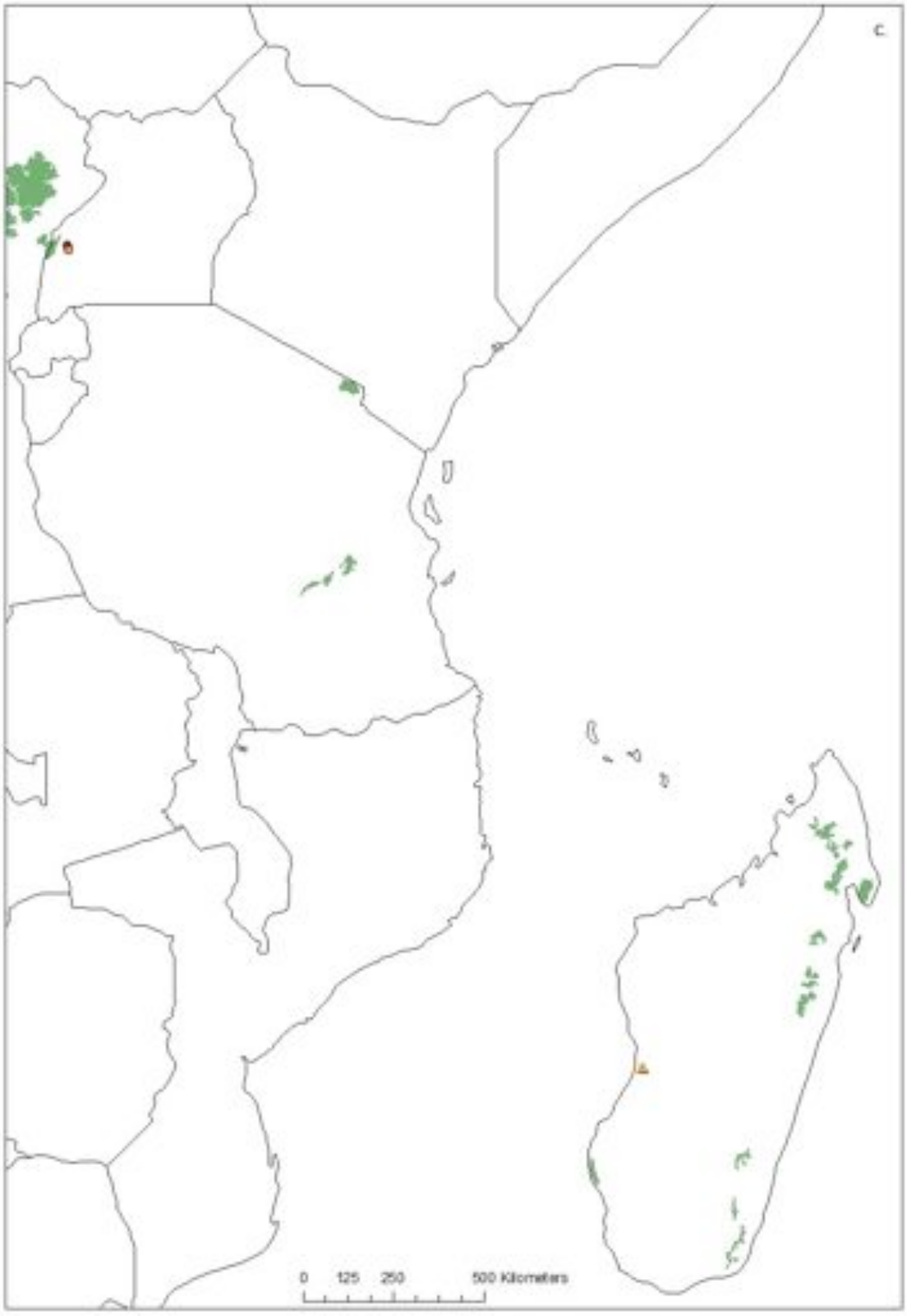

Figure 1. continued.

3.3.2. Data Analysis

In each site all trees over a specified DBH were measured in a plot to estimate AGB at two or more points in time. The minimum DBH cut-off across the 71 sites ranged from 1 cm to 10 cm, but was always consistent over time within a site. All analysis assumed a minimum DBH cut off of 1 cm DBH. For sites that had a minimum DBH of 2 cm (n=3), 2.5 cm (n=5), 3 cm (n=2) and 5 cm (n=23), data were left unchanged as the AGB stored in small stems was considered to be minimal. I recognise that AGB in these sites with be slightly underestimated, but bias is expected to be small.

To account for the missing AGB in small stems at sites that employed a higher minimum DBH (7 cm, n=1, or 10 cm, n=18), the ratio between the AGB of large (≥10 cm DBH): small (1 -10 cm DBH) stems was used. Therefore in the one site that used a DBH cut off of 7 cm AGB was slightly over estimated. To account for differences in the ratio of AGB in large: small stems in relation to forest age, data was split into three age classes; 1-10 years, 10-20 years, and >20 years, with the expectation that the ratio of large: small stem AGB in young forest plots would be higher than in older forest plots. A total of five sites reported AGB of large and small stems and were used to estimate large: small stem ratio (Table 13). All five sites used to calculate ratios were conducted in agricultural landscapes (permanent agriculture, shifting cultivation, and pasture), therefore estimated ratios were not used to calculate small stem AGB in logged forest studies, however this only effected one study by Toky and Ramakrishnan (1983).

Table 13. Ratio of large (≥10 cm DBH): small (1-10 cm DBH) stems used to standardise minimum DBH in each age class. Median in parentheses.

Source	1-10 years	10-20 years	>20 years
Hughes et al. (1999)	0.48 (0.48)	0.12 (0.12)	0.09 (0.06)
Costa et al. (2012)	-	0.10 (0.10)	-
Cifuentes-Jara (2008)	0.55 (0.50)	0.28 (0.16)	0.13 (0.10)
Marin-Spiotta et al. (2007)	-	-	0.05 (0.05)
This thesis chapter 3	-	0.29 (0.19)	-
Mean	0.51 (0.51)	0.20 (0.20)	0.09 (0.09)

Net AGB change in naturally regenerating forests is approximately an asymptotic function over time, with higher AGB accumulation in young forest, eventually declining in older forest. Therefore, for each site AGB accumulation was estimated using non-linear regression. Linear fits and different non-linear models (3-Paramater asymptotic exponential, 2-parameter exponential, Michalis-Menten and 4-parameter Weibull curves) were fitted to each site; the model with the lowest Akaike information criterion (AIC) was selected as the best fit to the data for each site. For each site the model with the best fit was used to predict AGB for every year, over the whole study duration. For each site the mean AGB accumulation rate for the first 10 years of recovery was calculated as:

$$\Sigma\ (y_2\text{-}y_1) + (y_3\text{-}y_2).....(y_{10}\text{-}y_9)/10$$

Where y_1 = predicted AGB at year 1, y_2 = predicted AGB at year 2 etc. (or slope coefficient in cases where this was the best fit). The AGB accumulation rates of sites were then compared using one-way analysis of variance (ANOVA) and post-hoc testing was conducted using Tukey's honest significant different (HSD) test.

I used linear mixed effects models to investigate if differing prior land use affected net AGB change over both the short-term (<20 yrs), and long-term (>20 yrs). Additional models were run with continent as a fixed factor to assess if biogeography impacts AGB recovery rates (no interaction was possible due to low replication), and climate variables as a fixed factor.

Two nested random effects, of site and plot, were used to account for the hierarchical structure of data collected at different spatial scales. The random effect of site referred to

each individual study site located across the tropics (Figure 10), with each individual site given a unique ID code. This site effect accounted for random variation in AGB accumulation, among sites, that could be due to differences in site conditions. The nested random effect of plot, referred to plots located within different sites. In sites, which used chronosequences, the same unique plot code was assigned to all plots in a chronosequence that were used to estimate a single regression line. In repeat measurement sites, the same unique plot code was assigned to one individual plot at each census, used to estimate a single regression line. That is, in repeat measurement sites, which had multiple plots, that were each measured more than once, each individual plot had its own unique plot code. This plot effect accounted for random variation in AGB accumulation among plots; it also identified individual repeat measure plots to avoid problems of non-independence.

All data used for mixed effects modelling was weighted, based on sampling effort, by plot size and study duration. Weighting was performed to ensured that studies which had been conducted over a larger area or over a longer time period, and therefore would likely have more accurate data, would be more influential in analysis. Weighting was calculated as:

Weight = $\sqrt{}$plot area (ha) + $\sqrt{}$ study duration (years)

All weights were then divided by the max value of the weights to constrain values between zero and one. In repeat measurement sites, study duration was taken as the number of years from the first to the last census. Whereas in chronosequence sites, study duration was taken as the difference between the maximum aged plot and the minimum aged plot. In sites where AGB measurements were a mean of multiple plots, I used total plot area (number of plots * plot area), to represent sampling effort.

To linearize data, the response variable of AGB and predictor variable of plot age, were both log transformed for analysis. Model simplification was conducted to assess the affects of land use and continent on AGB accumulation. AIC was used to determine the likelihood of a model being the most parsimonious to the data, using the function AICc, which account for small sample sizes, with the model with the lowest AICc value selected. AICc was implemented using the MnMIn package in R (Bartoń, 2015). Due to the multiplicative effect of log transforming both response and predictor variables, model coefficients, could not be back-transformed, to give the untransformed slope coefficient *b*. Therefore, instead I calculated the percentage increase in AGB for a doubling in time as:

Percentage increase = $(2\text{^}b^{-1}) \times 100$

Where b is the slope coefficient from the log-log mixed effects models.

Two separate analyses were conducted. Firstly, in short-term study sites, using data from all sites, only including data from plots ≤20 years old. A total of 61 sites had data from plots ≤20 years old, and were used in analysis. And additional four sites (DUP, MAD, RIS and URQ, see Appendix 1 for site codes) that only had data at one time point ≤20 years, were excluded, as a minimum of two time points were required to estimate AGB accumulation (criteria one). A second analysis was conducted in long-term study sites, which only used data from sites that had plots >20 years old. A total of 40 sites had data from plots >20 years old, the maximum age of plots in these sites was 100 years, with a mean of 43.8 years (± 5.8), therefore analysis of long-term sites was considered over a 40 year time period from 0 to 40 years. From these 40 sites, data from all sample plots was used, including data from plots <20 years old. This separate analysis of long-term study sites was conducted as non-linarites mean that forests are responding differently over the short and long-term. All linear mixed effects modelling was conducted using the lme function from the nlme package in R version 3.2.1 (Pinheiro et al., 2016, R Core Team, 2013).

3.4. Results

3.4.1. Distribution of data

My systematic review of AGB recovery literature yielded 68 studies and 71 individual sites, with 1669 individual measurements of AGB in naturally regenerating forests recovering following disturbance. A total of 48 (71%) sites came from Latin America, and 20 (28%) sites from Southeast Asia, and just three (4%) sites from Africa (Figure 10). Sites predominatly used cronosequence methods (n=53; 78%) rather than repeat measument methods (n=15; 22%). All 71 sites used in analysis were undergoing natural regeneration following one of four land use types; 1) cattle pasture, 2) permanent agriculture, which referred to sites undergoing large-scale agriculture that was not rotational, 3) shifting cultivation, which in this study includes rotation cultivation, and slash and burn agriculture sites, and finally 4) selective logging. The dominant land use type was shifting cultivation with 36 sites (Latin America = 21 sites, Asia = 13 sites, Africa = 2 sites), followed by cattle pasture with 19 sites, all conducted in Latin America (Figure 10). Large-scale permanent agriculture and selective logging made up 12% (n=9; Latin America = 5 sites, Asia = 3 sites, Africa = 1 site) and 10% (n=7; Latin America = 3 sites, Asia = 4 sites) of sites, respectively (Figure 10).

Maximum years of recovery (i.e. the age of the oldest plot in chronosequence studies, or the plot age in the last census in repeat measurement studies) for each site ranged from 1.9 to 100, with a mean of 26.7 years (± 4.8, 95% CI) and a median of 27 years (Figure 11a). Of the four land use types, maximum years of recovery was highest in pasture sites (mean = 40.6 years, median = 35.5 years), and lowest in logging sites (mean = 24.4 years, median = 17.5 years; Figure 12a), however there was no significant difference in maximum years of recovery among land use types.

Study duration (i.e. duration in years from; youngest plot to oldest plot in chronosequence studies, or first census to last census in repeat measurement studies) for each site ranged from one to 80 years, with a mean of 26.7 years (± 4.6, 95% CI), and a median of 23 years range (Figure 11b). Study duration was also highest in pasture sites (mean = 35.6 years,

median = 32 years), and lowest in logging sites (mean = 18 years, median = 8 years; Figure 12b), again there was no significant difference among land use types.

The duration of land use prior to abandonment and recovery, ranged from 0 to 60 years, with a mean of 9.4 years (± 3.1) and median of 4 years (Figure 11c). The duration of land use prior to abandonment was highest in pasture sites (mean = 16.9 years, median = 13 years), followed by shifting cultivation (mean = 10.3 years, median = 5 years), and permanent agriculture sites (mean = 4.9 years, median = 2.8 years; Figure 12c). Land use duration in logged forest was zero as forest were immediately abandoned and left to naturally regenerate following selective logging. However, no significant differences in duration of land use prior to abandonment among land uses were observed.

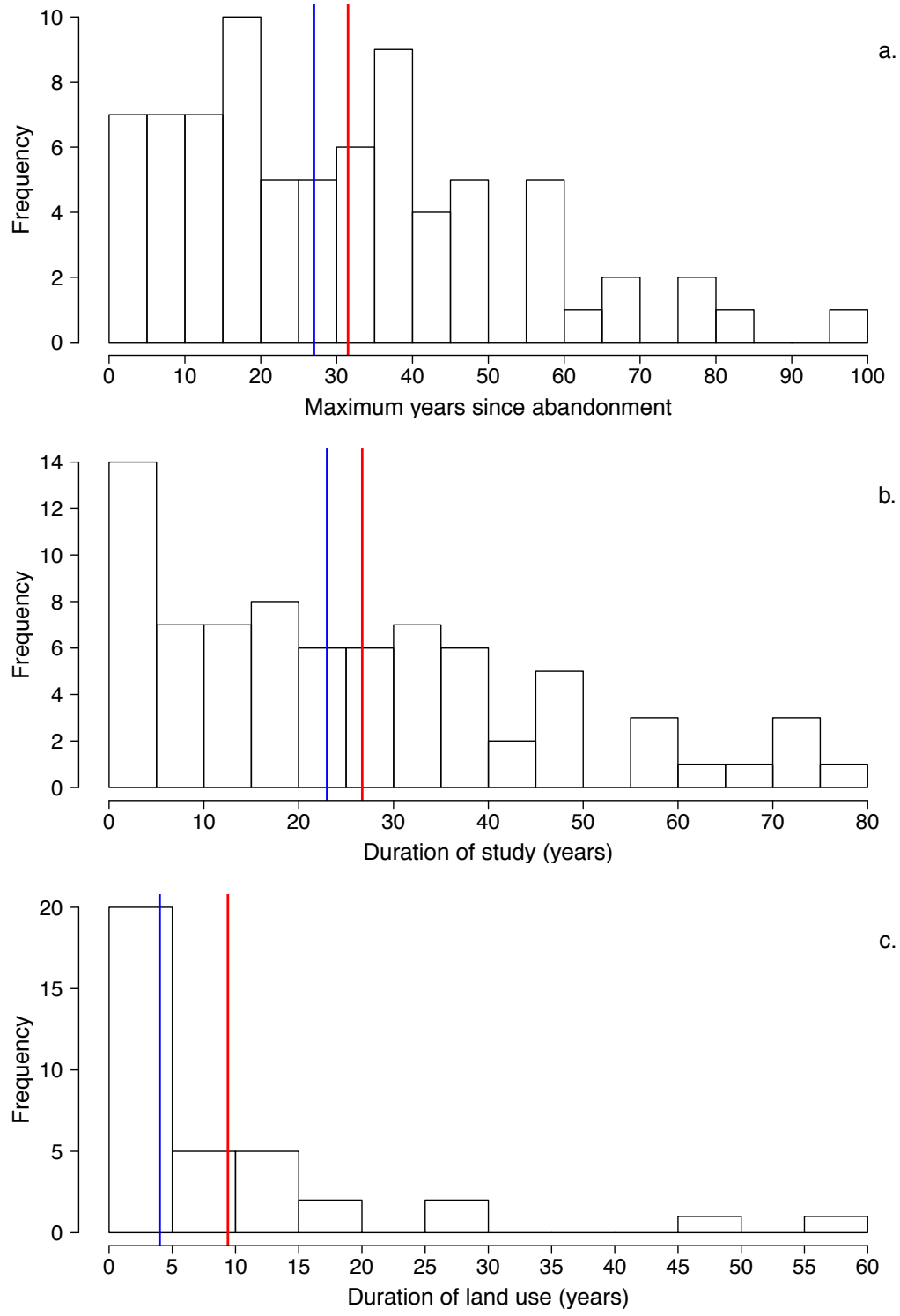

Figure 11. Histogram of a. years since abandonment, b. duration of study (years) and c. duration of land use (years). Red line shows mean and blue line shows median.

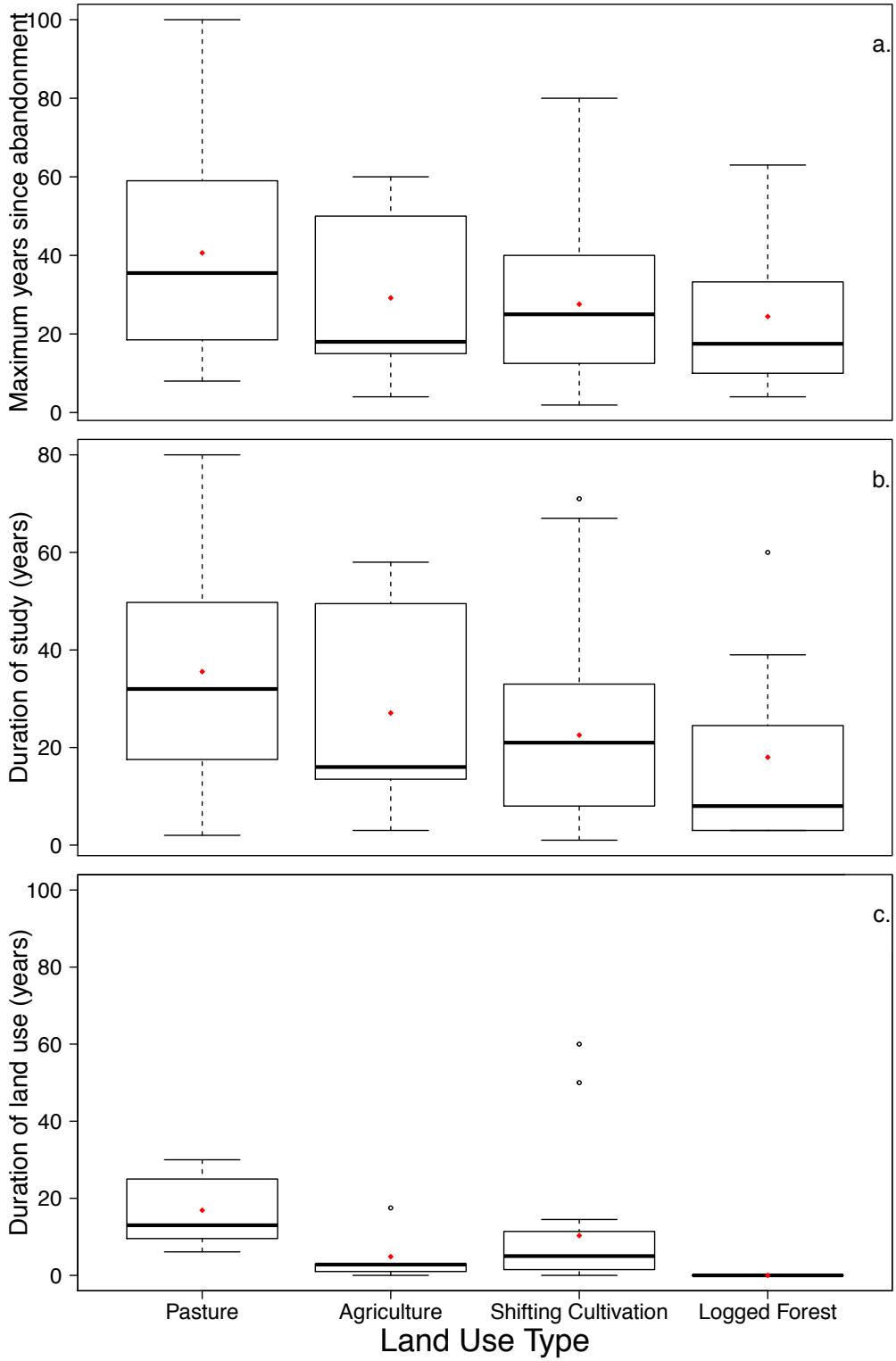

Figure 12. Boxplots of a. years since abandonment, b. duration of study (years) and c duration of land use (years), split by degradation type. Red points show mean.

3.4.2. AGB accumulation

The AGB accumulation of different sites, in the first ten years after abandonment, was highly variable, with a weighted mean of 4.8 Mg ha^{-1} yr^{-1} (± 1.3, 95% CI; weighted by sampling effort, un-weighted mean = 5.9 Mg ha^{-1} yr^{-1}), ranging from -0.9 Mg ha^{-1} yr^{-1} to 36 Mg ha^{-1} yr^{-1}. The extremely high maximum rate of 36 Mg ha^{-1} yr^{-1} was estimated from a site chronosequence site, with just two plots aged seven and eight years (d'Oliveira et al., 2011), this site was therefore excluded from further analysis. There was no significant difference in the mean AGB accumulation in different land use types ($F = 0.26$, $df = 3$, $p = 0.86$), with mean AGB accumulation ranging from 4.2 Mg ha^{-1} yr^{-1} in Logging sites to 6.1 Mg ha^{-1} yr^{-1} in Agriculture sites (Figure 13).

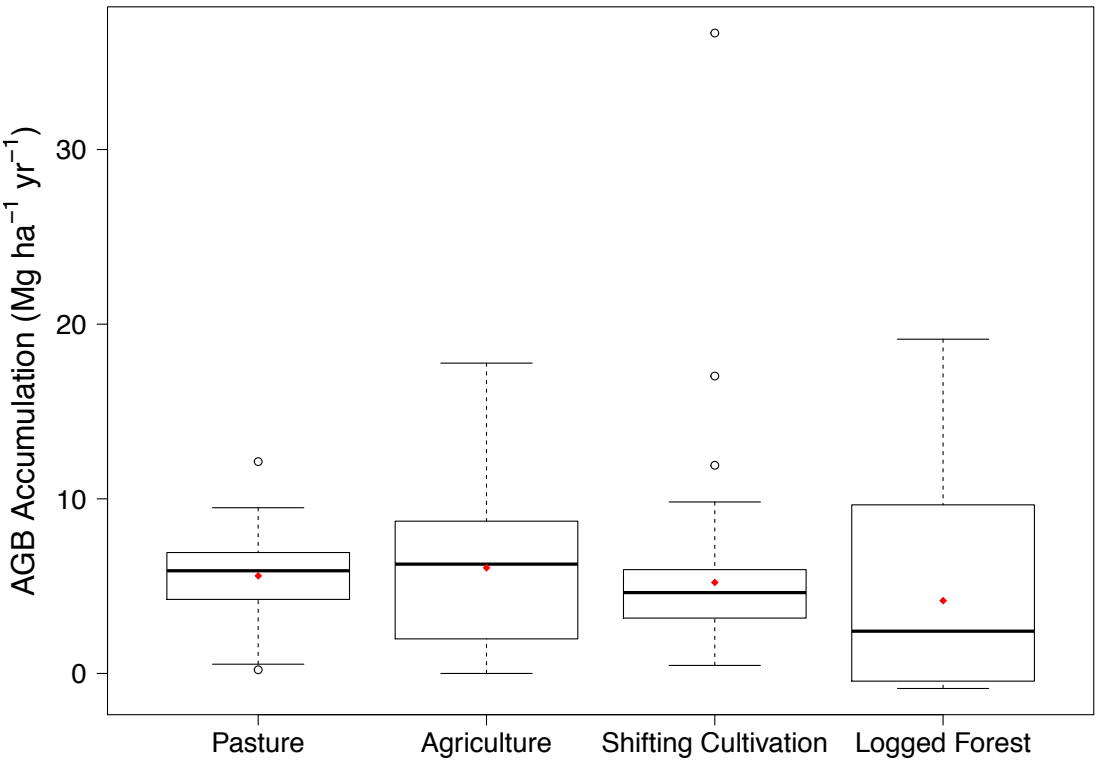

Figure 13. Boxplot showing AGB accumulation for all sites split by degradation type. Red points show mean.

In general the relationship between net AGB change and the number of years since abandonment in all agricultural land use types (pasture, agriculture and shifting cultivation), appeared to be slowing over time (Figure 14). However, in logged forest the relationship between AGB and recovery was highly variable amongst sites (Figure 14). Unsurprisingly, initial AGB in logged forests was generally higher then observed in other

land use types (Figure 14), with logged forest plots having a significantly higher intercept (F = 7.1, df = 3, p = <0.001) at year zero, of 108.8 Mg ha^{-1}, compared to other land use types (pasture sites, intercept = 6.2 Mg ha^{-1}, p = <0.001; shifting cultivation sites, intercept = 0.5 Ma ha^{-1}, p = <0.001; permanent agricultural sites, intercept = 9.1 Mg ha^{-1}, p = 0.005). Due to the large differences in AGB in logged forest sites compared to agricultural land use types, logged forest sites were excluded from subsequent analysis. Furthermore, there were only seven logged forest site, meaning that logged forest were poorly represented in the dataset.

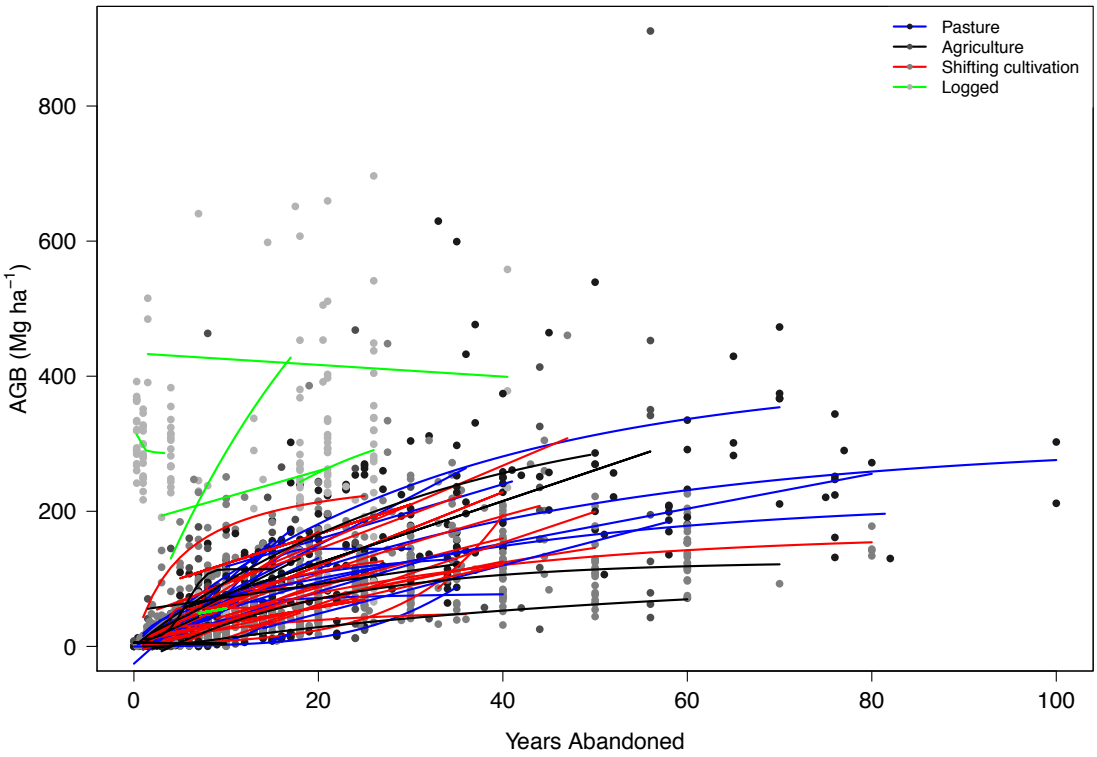

Figure 14. Relationship between total AGB and years abandoned, split by degradation type. Each line shows the AGB accumulation for a different study.

3.4.3. Effect of land use on forest recovery

In the first 20 years of recovery AGB increased significantly (slope = 1.3 ± SE 0.1, p = <0.001, Figure 15a), from 1.8 Mg ha^{-1} in year 1 to 100.3 Mg ha^{-1} in years 20 (Figure 15b), this equated to a 155.5 % increase in AGB for a doubling in time, or a rate of ~4.9 Mg ha^{-1} yr^{-1}. However, land use type did not affect AGB recovery trajectory, with model 2c, which

excluded land use, being the most parsimonious (Table 14). The random effect of site explained 73% of residual variation, compared to 15% explained by the random effect of plot.

Using long-term studies, AGB recovery over 40 years also increased significantly (slope = 1.1 ± 0.1, p = <0.001, Figure 16a), from 3.2 Mg ha^{-1} in year 1 to 171.8 Mg ha^{-1} in year 40 (Figure 16b), this equated to a 112.8 % increase in AGB for a doubling in time, or rate of ~4.3 Mg ha^{-1} yr^{-1}, lower than the AGB accumulation rate estimated for the first 20 years of recovery, suggesting that AGB accumulation is higher in young forest sites (≤20 years old) than old forest sites (>20 years old). As with short-term studies, there was no affect of land use type of recovery trajectory, with model 6c being the most parsimonious (Table 14). The random effect of site explained twice as much (40%) of the residual variation, compared to the random effect of plot (19%).

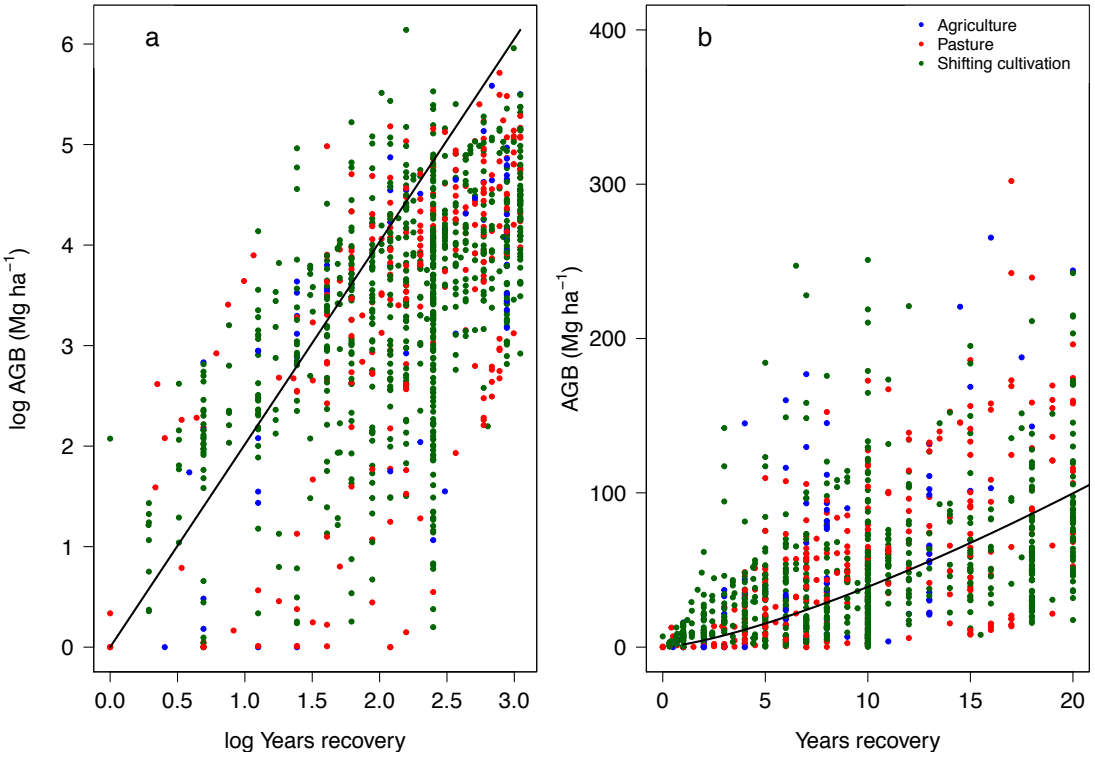

Figure 15. Relationship between a) log years recovery and log AGB, and b)years recovery and AGB, in short-term sites (0-20 years recovery), line shows fit from model 2c.

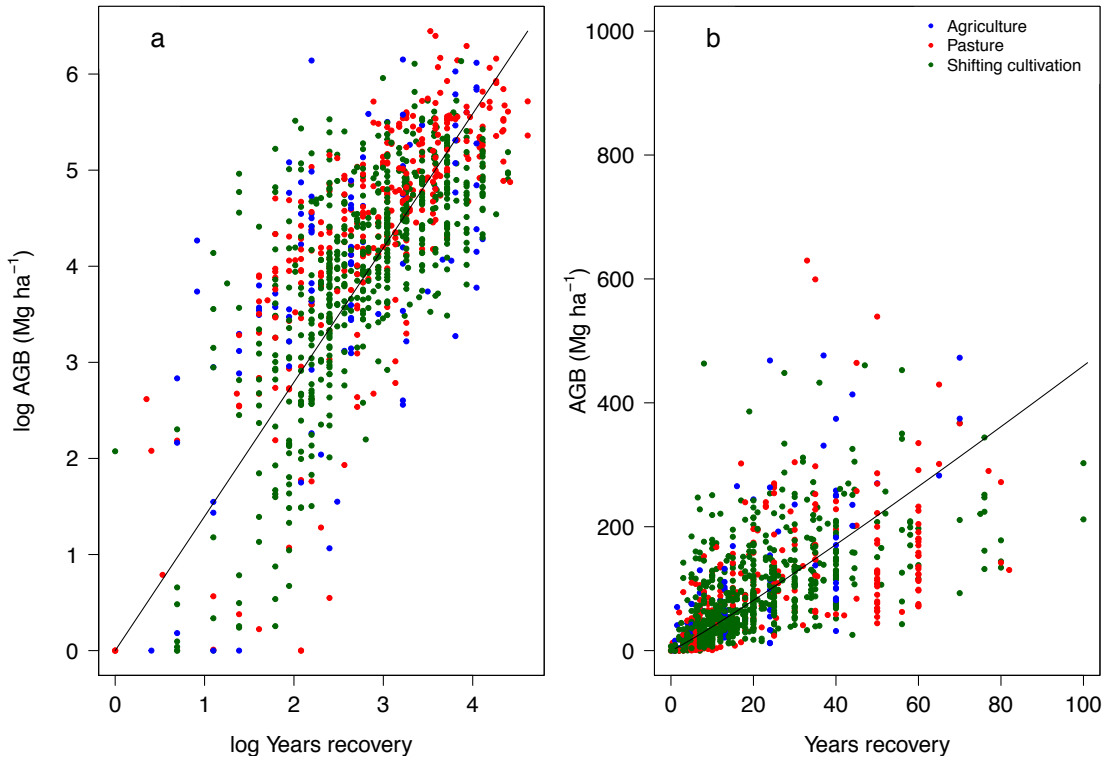

Figure 16. Relationship between a) log years recovery and log AGB, and b)years recovery and AGB, in long-term sites (0-100 years of recovery), line shows fit from model 6c.

Table 14. Description of Linear mixed effect models tested, the degrees of freedom, AICc and log likelihood, for short-term and long-term sites.

Model	Variables	DF	AICc	Log likelihood
	Short-term sites (0-20 years)			
1a	AGB~Years * Land Use	13	10548.0	-5261.0
1b	AGB~Years + Land Use	11	10546.3	-5262.1
1c	AGB~Years	9	10544.0	-5263.0
2a	Log(AGB)~Log(Years)* Land Use	13	2350.9	-1162.4
2b	Log(AGB)~Log(Years) + Land Use	11	2347.1	-1162.6
2c	**Log(AGB)~Log(Years)**	**9**	**2344.0**	**-1163.0**
3a	AGB~Years * Continent	13	10681.5	-5327.8
3b	AGB~Years + Continent	11	10678.3	-5328.1
3c	AGB~Years	9	10679.1	-5330.5
4a	Log(AGB)~Log(Years)* Continent	13	2339.1	-1156.6
4b	**Log(AGB)~Log(Years) + Continent**	**11**	**2339.3**[a]	**-1158.6**
4c	Log(AGB)~Log(Years)	9	2354.6	-1168.3
N1	Null model (Log)AGB~1	8	2433.7	-1208.9
	Long-term sites (0-40 years)			
5a	AGB~Years * Land Use	13	11160.8	-5567.399
5b	AGB~Years + Land Use	11	11157.13	-5567.564
5c	AGB~Years	9	11153.35	-5567.676
6a	Log(AGB)~Log(Years)* Land Use	13	2056.634	-1015.317
6b	Log(AGB)~Log(Years) + Land Use	11	2052.802	-1015.401
6c	**Log(AGB)~Log(Years)**	**9**	**2049.214**	**-1015.607**
7a	AGB~Years * Continent	13	11156.97	-5565.483
7b	AGB~Years + Continent	11	11154	-5565.999
7c	AGB~Years	9	11153.35	-5567.676
8a	**Log(AGB)~Log(Years)* Continent**	**13**	**2047.024**	**-1010.512**
8b	Log(AGB)~Log(Years) + Continent	11	2050.695	-1014.347
8c	Log(AGB)~Log(Years)	9	2049.214	-1015.607
N2	Null model (Log)AGB~1	8	2122.055	-1053.027

Models in bold were the minimum adequate model following model simplification compared using maximum likelihood. A = Model 4b had slightly higher AICc, than model 4a but was not significantly different therefore the simple model (4b) was selected.

3.4.4. Effect of continent on forest recovery

Continents did not differ significantly in net AGB change (model4b, Table 14), but they did, differ in intercept, with African sites recovering from a significantly lower AGB, than Southeast Asian (T = 6.6, df = 53, p = <0.001) or Latin American Sites (T = 6.4, df = 53, p =<0.001; Figure 17). The random effects of site and plot explained a similar amount of residual variation (28% and 29%, respectively). In long-term sites however, net AGB change was significantly different among continents, with Latin American sites having a significantly lower AGB accumulation rate (n = 30; slope = 1.0 ± 0.1, p = <0.001, Figure 18), compared to Southeast Asian sites (n = 9, slope = 1.4 ± 0.2; Americas vs. Southeast Asia T = 1.9, df = 965, p = 0.05, Figure 18), and African sites (n = 1, slope = 2.0 ± 0.5; Americas vs. Africa T = 2.1, df = 965, p = 0.04, Figure 18). After 40 years recovery, Southeast Asian sites had the highest AGB, reaching 243.5 Mg ha^{-1}, with AGB increasing by 156.6 % for a doubling in time, Latin American sites had reached 161.3 Mg ha^{-1}, which equated to a 101.1 % increase in AGB for a doubling in time. African sites had the highest rate of increase (291.0 % for a doubling in time), however after 40 years recovery, they had the lowest AGB at 117.8 Mg ha^{-1}, due to a significantly lower intercept compared to Latin American (T = -2.2, df = 965, p = 0.03) sites, meaning that they were recovering from a much lower AGB. The site random factor explained 54% of residual variation, whilst plot explained <1%.

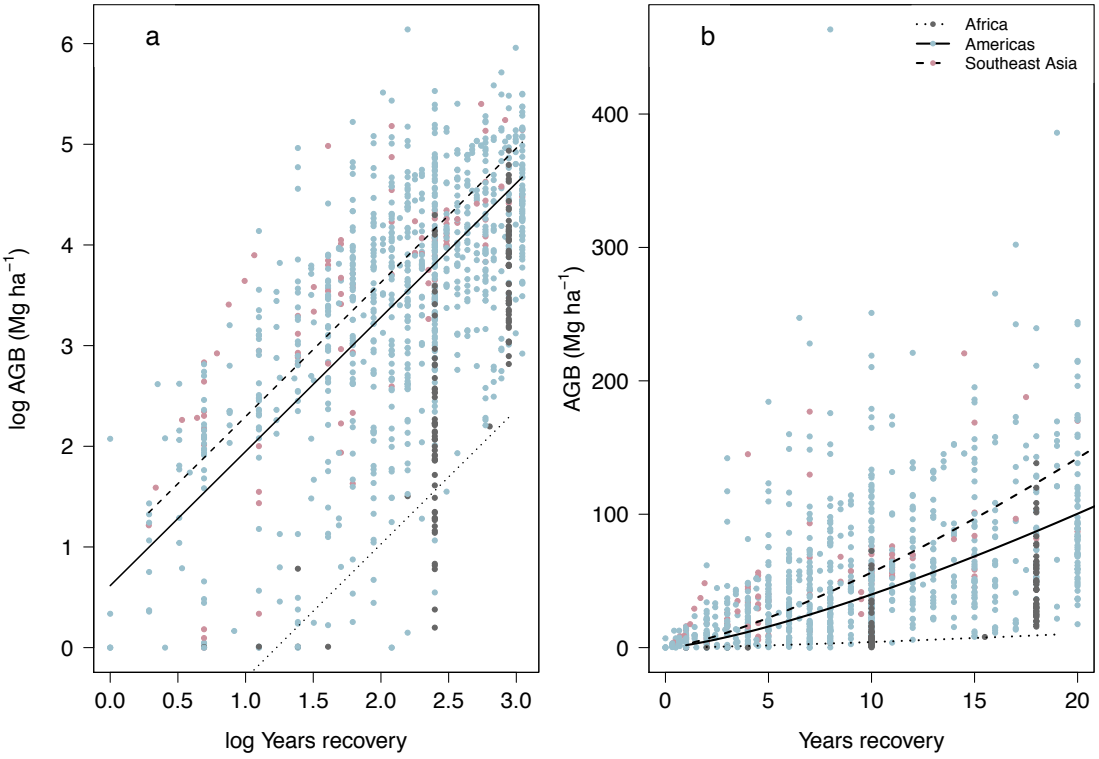

Figure 17. Relationship between a) log years recovery and log AGB, and b)years recovery and AGB, in each continent, in short-term sites (0-20 years recovery), lines show fit from model 4b for each continent.

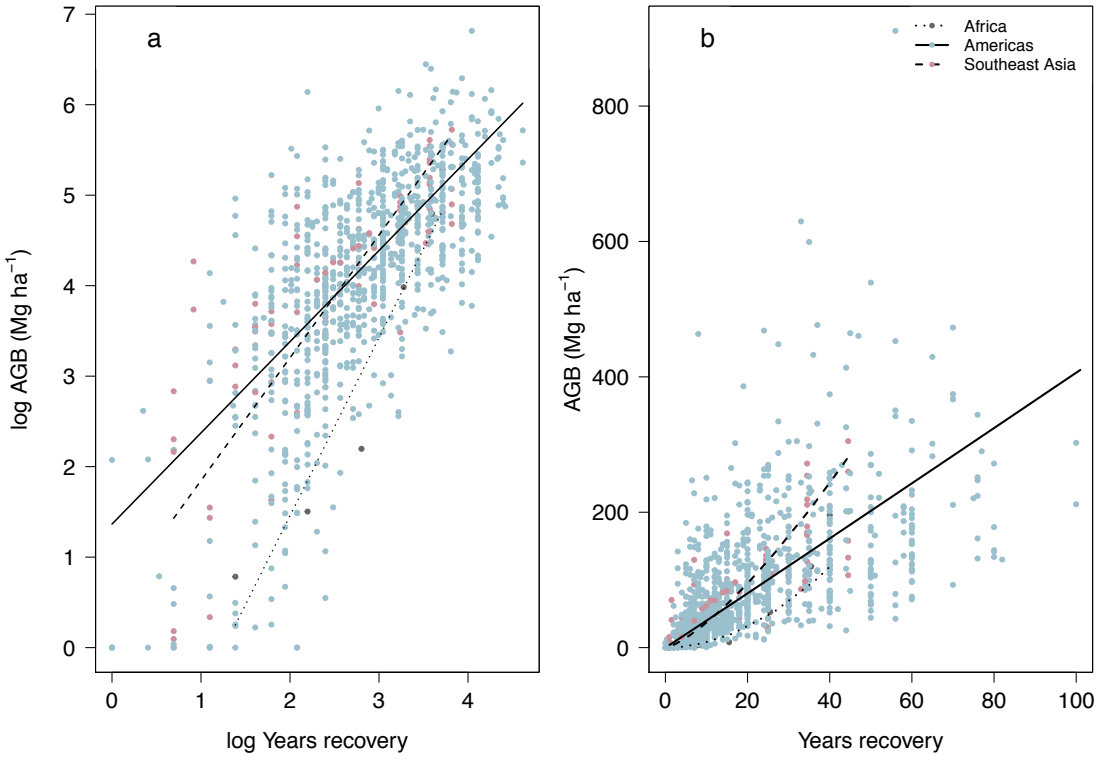

Figure 18. Relationship between a) log years recovery and log AGB, and b)years recovery and AGB, in each continent, in long-term sites (0-100 years recovery) , lines show fit from model 8a for each continent.

3.4.5. Effects of climate on forest recovery

When climate variables were added to mixed effects models there was strong collinearity between MAP and DRYQ (Pearson correlation = 0.7, T = 34.4, df = 1050, p = <0.001), however in all cases MAP had a slightly better fit to the data, therefore only MAP was used in analysis of climate data. When effects of land use and climate were added to models, there was still no significant relationship between land use and AGB accumulation, however, in short-term sites there was a significant positive effect of MAP on AGB (T = 3.7, df = 904, p = <0.001, Table 15), but no effect of MAT. A significant positive effect of MAP was also observed in long-term sites (T = 3.9, df = 388, p = <0.001, Table 15). In both short and long-term sites the random factor site explained a greater proportion of residual variation (36% and 43%, respectively), compared to plot (22% and 16%, respectively).

In short-term sites when the effects of continent and climate were added to models, the significant effect of continent on AGB was still observed however, MAP also had a significant positive effect on AGB accumulation (model 10d; T = 3.2, df = 904, p = 0.002; Table 15). In short-term sites, 25% of residual variation was explained by site and 31% by plot. In long-term sites, when climate data is added to the model, the significant effect of continent on AGB accumulation is no longer present, with model 11f being the most parsimonious (Table 15). However, there is a significant effect of MAP on AGB accumulation (T = 3.9, df = 388, p = <0.001). In long-term sites, 43% of residual variation was explained by site and 16% by plot

Table 15. Description of Linear mixed effect models, including climate variables. Showing the degrees of freedom, AICc and log likelihood, for short-term and long-term sites.

Model	Variables	DF	AICc	Log likelihood
	Young sites (0-20 years)			
9a	Log(AGB)~Log(Years)*Land Use+MAP*MAT	16	2271.0	-1119.5
9b	Log(AGB)~Log(Years)*Land Use+MAP+MAT	15	2270.2	-1120.1
9c	Log(AGB)~Log(Years)+Land Use+MAP+MAT	13	2266.2	-1120.1
9d	Log(AGB)~Log(Years)+Land Use+MAP	12	2266.2	-1121.1
9e	Log(AGB)~Log(Years)+Land Use	11	2277.4	-1127.7
9f	**Log(AGB)~Log(Years)+MAP**	**10**	**2263.9**	**-1121.9**
10a	Log(AGB)~Log(Years)*Continent+MAP*MAT	16	2251.7	-1109.9
10b	Log(AGB)~Log(Years)*Continent+MAP+MAT	15	2253.7	-1111.8
10c	Log(AGB)~Log(Years)+Continent+MAP+MAT	13	2253.5	-1113.7
10d	**Log(AGB)~Log(Years)+Continent+MAP**	**12**	**2251.5**	**-1113.8**
10e	Log(AGB)~Log(Years)+Continent	11	2259.4	-1118.7
9f	Log(AGB)~Log(Years)+MAP	10	2263.9	-1121.9
	Log(AGB)~Log(Years)	9	2274.3	-1128.2
	All years (0-40 years)			
11a	Log(AGB)~Log(Years)*Land Use+MAP*MAT	16	453.0	-210.5
11b	Log(AGB)~Log(Years)*Land Use+MAP+MAT	15	453.5	-211.7
11c	Log(AGB)~Log(Years)+Land Use+MAP+MAT	13	451.4	-212.7
11d	Log(AGB)~Log(Years)+Land Use+MAP	12	449.6	-212.8
11e	Log(AGB)~Log(Years)+Land Use	11	463.1	-220.6
11f	**Log(AGB)~Log(Years)+MAP**	**10**	**447.2**	**-213.6**
12a	Log(AGB)~Log(Years)*Continent+MAP*MAT	16	448.5	-208.2
12b	Log(AGB)~Log(Years)*Continent+MAP+MAT	15	451.2	-210.6
12c	Log(AGB)~Log(Years)*Continent+MAP	14	449.0	-210.5
12d	Log(AGB)~Log(Years)*Continent	13	462.2	-218.1
12e	Log(AGB)~Log(Years)*MAP	11	449.2	-213.6
12f	Log(AGB)~Log(Years)+Continent+MAP+MAT	13	452.8	-213.4
12g	Log(AGB)~Log(Years)+Continent+MAP	12	451.1	-213.5
12h	Log(AGB)~Log(Years)+Continent	11	463.9	-221.0
11f	**Log(AGB)~Log(Years)+MAP**	**10**	**447.2**	**-213.6**
	Log(AGB)~Log(Years)	9	460.1	-221.0

Models in bold were the minimum adequate model following model simplification compared using maximum likelihood.

3.5. Discussion

This systematic review of 68 studies found a mean AGB accumulation rate of 5.9 Mg ha^{-1} yr^{-1} (± 1.3), and a weighted mean of 4.8 Mg ha^{-1} yr^{-1} (weighted by sampling effort), across all land use types. In agricultural land use types only (pasture, agriculture and shifting cultivation), short-term sites (0-20 years old), had an AGB accumulation of approximately 4.9 Mg ha^{-1} yr^{-1}. This is slightly lower than the 6.1 Mg ha^{-1} yr^{-1}, reported by Poorter et al. (2016), for the first 20 years of recovery in abandoned agriculture, in the Neotropics, and the 7.7 Mg ha^{-1} yr^{-1}, reported by Bonner et al. (2013), for the first 18 years of recovery in abandoned agriculture, across the tropics. These differences in AGB accumulation rate are likely due to differences in data and methodologies used. Whilst there is very little overlap between the studies used in Poorter *et al*. and Bonner *et al*. (four studies in common), there is a great deal of overlap between the studies used in my analysis and both Poorter *et al*. (n = 20) and Bonner *et al*., (n = 22). However, this chapter analyses data from 32 additional studies, which were not included in either Poorter *et al*. or Bonner *et al*., more than doubling the number of studies used in analysis. Additionally, Bonner *et al.* used meta-analysis techniques to estimate AGB accumulation, whilst Poorter *et al.* estimated AGB from the original plot data and predicted AGB accumulation from each study using non-linear regression. Whereas this review employed mixed-effects modelling techniques. Mixed-effects models are commonly employed in the field of ecology (Bolker et al., 2009), and were considered appropriate for analysis, as they are able to account for the hierarchical structure of data, from different sites and plots (Gelman and Hill, 2006).

In long-term sites, I estimated an AGB accumulation rate of approximately 4.3 Mg ha^{-1} yr^{-1}, again this is slightly lower than the AGB accumulation rate of 5.8 Mg ha^{-1} yr^{-1}, predicted by Bonner et al. (2013), in sites >18 years old. However, similar trends were observed between this analysis and Bonner *et al*., with a faster AGB accumulation in younger plots (<20 years old) compared to older plots. Similar trends of reducing AGB accumulation with forest age have also been observed in some individual studies included in this analysis. For example, in lands recovering following shifting cultivation Eaton and Lawrence (2009) found AGB accumulation rates of 5.8 Mg ha^{-1} yr^{-1} in the first five years of recovery, which slowed to 1.5 Mg ha^{-1} yr^{-1} after 25 year of recovery. In agriculture sites

Alves et al. (1997) found an AGB accumulation rate of 8.4 Mg ha^{-1} yr^{-1} in the first 10 years of recovery, slowing to 7.4 Mg ha^{-1} yr^{-1} between 11 and 18 years. The large variability in AGB accumulation estimates from individual site shows the importance of conducting large-scale quantitative analysis of literature, however, these studies suggest that AGB accumulation shows a decreasing trend over time, supporting the assumption that AGB accumulation is asymptotic over time. Initially high rates of AGB accumulation are likely due to increases in stem density, leading to higher rate of photosynthesis, over time some AGB will be lost to mortality, causing a decline in net AGB change. Thus, older forest may have similar woody production to younger forests, but woody production in older forest is being offset by mortality, meaning changes in net AGB stocks will reduce.

Somewhat surprisingly, there was no effect of prior land use type on the subsequent recovery trajectory of AGB, with all land uses accumulating AGB at the same rate. This is unexpected, as it is widely thought that the recovery of naturally regenerating forest is influenced by the severity of disturbance (Chazdon, 2003, Guariguata and Ostertag, 2001). It would be expected that pasture areas, would have slower growth rates due to the complete removal of natural vegetation and the planting of non-native grasses for grazing (Buschbacher, 1986), in comparison to shifting agriculture, performed on a rotational basis, which during fallow periods allows nutrients to accumulate in the soil and vegetation to regrow (Fox, 2000). A study by Fearnside and Guimarães (1996) found this to be the case, with higher rate of AGB accumulation in shifting cultivation sites compared to pasture sites at 7.3 Mg ha^{-1} yr^{-1} and 5.3 Mg ha^{-1} yr^{-1}, respectively, over a 20 year time period. Other studies have also observed impacts of land use intensity on AGB recovery, Uhl et al. (1988), found that pastures cleared by bulldozer had recovered just 4.7 Mg ha^{-1} of AGB, eight years after abandonment, compared to 88.9 Mg ha^{-1} in manually cleared pastures. Slower natural regeneration of forest in more severely degraded land has been attributed to more heavily degraded soil, poorer soil seed bank and dispersal limitations (Cubiña and Aide, 2001, Holl, 1999, Martínez and Zinck, 2004). This study compares three land use categories, which have relatively broad definitions, and therefore this analysis may not be able to detect differences in land use intensity, furthermore, effects of intensity may be confounded by continental differences, for example, all pasture sites were in Latin America (Figure 10).

Whilst there were no clear effects of land use on AGB recovery trajectories, there were significant differences in recovery among continents. In long-term sites, Latin American sites had the lowest AGB accumulation, followed by Southeast Asian sites, and African

sites having the fastest AGB accumulation (Figure 18), however in short-term sites no significant differences in AGB accumulation were observed. These findings differ slightly from those of Bonner et al. (2013), who only found significant differences in young forest plots (<18 years old) and not older forest plots (>18 years old), as seen in this study. In young forest plots Bonner *et al*. found that Southeast Asian studies had significantly lower AGB accumulation compared to Latin America and Africa, attributing this to higher population density in Southeast Asia, which could drive more intense land use prior to abandonment. In this study the opposite was true with Latin American sites having slower AGB accumulation than Southeast Asian sites, possibly due to the lower rates of net primary productivity found in Latin American forest (Malhi, 2012)

Bonner et al. (2013) noted a distinct bias of studies towards Latin America. Whilst my study suffers from the same bias with 45 sites in Latin America, 16 in Southeast Asia and just three in Africa (excluding logging sites), this thesis chapter is nevertheless based on a larger number of sites than Bonner *et al*. (45 vs. 15 in Latin America, 16 vs. 7 in Southeast Asia and 3 vs. 1 in Africa, respectively), therefore it is possible that the predicted AGB accumulation rates presented in this chapter offer an improved estimation of AGB recovery. The exception to this is Africa. The apparently higher rate of AGB accumulation observed in Africa is based on just a single long-term study (Raharimalala et al., 2012) from Madagascar, which monitored AGB change in shifting cultivation sites over 40 years, and is unlikely to be representative of AGB accumulation in naturally regenerating forest following varied land use change interventions across Africa. My study highlights the extreme paucity of data investigating the recovery of African lands following disturbance. Notably, of the three African studies I include, one is using the data presented in chapter three of this thesis (Appendix 10, Wheeler et al., 2016), which was conducted in an actively restored forest site, rather than naturally regenerating forest, and therefore may have elevated levels of AGB accumulation as a result of management interventions.

The significant positive effect of MAP on AGB in the models removed any impact of continents in short and long-term sites. A positive relationship between AGB and precipitation makes theoretical sense, as photosynthetic rates tend to be higher in wetter areas, which leads to high plant productivity (Guan et al., 2015), wetter forest would not have a restricted growing season as observed in some seasonally dry tropical forests (Condit et al., 2004), and they would be less susceptible to fire (Cochrane et al., 1999). Significant positive effects of MAP on AGB were also observed by Poorter et al. (2016),

they estimated that following 20 years of natural regeneration: wet forest (>2500 mm yr^{-1}) had on average 28 Mg ha^{-1} more AGB, than dry forest (<1500 mm yr^{-1}). Toledo et al. (2011) also observed a positive correlation between tree growth rate and rainfall, alongside a negative correlation with dry season length (months), in logged forest sites in Bolivia. However, these same trends were not seen by Bonner et al. (2013), who found no significant effect of either MAP or precipitation seasonality (coefficient of variation) on AGB accumulation, this is possibly because all studies used in their analysis were from moist or wet sites, with MAP ranging from 1400 mm yr^{-1} to 7000 mm yr^{-1}, whereas my analysis also includes dry sites with MAP below 1000 mm yr^{-1} (ranging from 835 mm yr^{-1} to 5200 mm yr^{-1}).

The MAP of sites in each continents follows expected trends (Hijmans et al., 2005, Malhi and Wright, 2004), with African sites being the driest (MAP = 1125 mm yr^{-1}), followed by Latin America (MAP = 2169 mm yr^{-1}), with Southeast Asian sites being the wettest (MAP = 2646 mm yr^{-1}). Due to these continental differences in MAP, it is possible that the differences in AGB accumulation observed between continents were actually related to differences in climate. Southeast Asian sites had apparently higher AGB accumulation rates than Latin American sites; this would be expected if there were higher MAP, as sites would not be rainfall limited, allowing for higher rates of gross primary productivity (Malhi, 2012), indeed increases in AGB along rainfall gradients have been observed (Malhi et al., 2006, Slik et al., 2010, Becknell et al., 2012), however these effects saturate in areas with very high MAP. Whereas drier sites, which have a restricted growing season, due to high intra-annual rainfall seasonality would be expected to have slower AGB accumulation (Becknell et al., 2012). However, African sites, which have the lowest MAP but the highest AGB accumulation do not fit with this trend. Again, caution must be taken when considering results from Africa as they are based on a single site. It is possible that other factors, such as soil fertility, acting at the site-specific scale might be facilitating high AGB accumulation in this particular site.

The number of years of recovery is by far the most important predictor of AGB, however MAP also appears to have a significant positive effect on AGB accumulation. This finding could have important implications for the carbon sequestration potential of naturally regenerating forest. Particularly in light of the possible increases in drought events predicted in parts of the tropics over the coming decades, as a result of climate change

(Malhi et al., 2008, Cai et al., 2014), with reductions in rainfall possibly resulting in reductions in AGB accumulation rates.

However, overall I predict fast rates of recovery in naturally regenerating forest, with forests reaching approximately 100 Mg ha^{-1} after 20 years of recovery, and 171 Mg ha^{-1} after 40 years of recovery. AGB in naturally regenerating forests at 40 years is equivalent to 58% of primary forest AGB (296.4 Mg ha^{-1}), if the AGB accumulation rate of 4.3 Mg ha^{-1} yr^{-1} estimated for long-term sites were to continue, then naturally regenerating forest would reach 90% of primary forest AGB levels in 60 years. This time period is slightly faster than the 66 years to recovery 90% of primary forest AGB estimated by Poorter et al. (2016). Another review by Martin et al. (2013) estimated it would take secondary forests 85 years to recovery 83% of primary forest AGB, again slower than estimated in my analysis. Neither of these studies report the AGB of reference primary forest used in analysis, therefore the shorter time period of 60 years estimated in my analysis, could be due my study having a lower AGB in primary forest.

Whilst this study shows that prior land use does not affect recovery rates of AGB in naturally regenerating forest on average, there are particular cases when AGB accumulation would be reduced, and may require management interventions to aid recovery (Chazdon, 2008). Areas in a state of arrested succession, for example, due to repeated burning or heavy invasion by exotic species, may require management interventions to help alleviate these problems and speed up recovery. Such interventions may include fire management, removal of invasive species, or planting of native seedlings (Lamb et al., 2005). Therefore, it may be possible to increase the rates of forest recovery by undertaking active restoration of disturbed areas.

3.6. Conclusions

Forests naturally regenerating on disturbed lands are able to rapidly sequester carbon and therefore offer a potentially important means of increasing terrestrial carbon storage, with relatively high AGB found in naturally regenerating forest after 40 years of recovery, and reaching 90% of primary forest AGB in 60 years. Therefore if naturally regenerating forests are left to recover over a large enough area they could present a potentially important climate change mitigation strategy.

Precipitation is an important factor influencing the rate of AGB recovery and must be considered in the face of a changing climate in the tropics, which could possibly lead to higher frequencies of drought. However, promoting the natural regeneration of disturbed lands and protecting naturally regenerating forest, should be encouraged over a large spatial scale, as natural regeneration could offer large climate change mitigation benefits.

4. Carbon Sequestration and Tree Diversity Following 18 Years of Active Tropical Forest Restoration in Kibale National Park

4.1. Abstract

Vast areas of degraded tropical forest, combined with increasing interest in mitigating climate change and conserving biodiversity, demonstrate the potential value of restoring tropical forest. However, there is a lack of long-term studies assessing active management for restoration. Here we investigate above-ground biomass (AGB), forest structure, and biodiversity, before degradation (in old-growth forest), after degradation (in abandoned agricultural savanna grassland), and within a forest that is actively being restored in Kibale National Park, Uganda. In 1995 degraded land in Kibale was protected from fire and replanted with native seedlings (39 species) at a density of 400 seedlings ha^{-1}. Sixty-five plots (50 m x 10 m) were established in restoration areas in 2005 and 50 of these were re-measured in 2013, allowing changes to be assessed over 18 years. Degraded plots have an Above Ground Biomass (AGB) of 5.1 Mg dry mass ha^{-1}, of which 80% is grass. By 2005 AGB of trees ≥10 cm DBH was 9.5 Mg ha^{-1}, increasing to 40.6 Mg ha^{-1} by 2013, accumulating at a rate of 3.9 Mg ha^{-1} $year^{-1}$. A total of 153 planted individuals ha^{-1} (38 %) remained by 2013, contributing 28.9 Mg ha^{-1} (70%) of total AGB. Eighteen years after restoration, AGB in the plots was 12% of old-growth (419 Mg ha^{-1}). If current accumulation rates continue restoration forest would reach old-growth AGB in a further 96 years. Biodiversity of degraded plots prior to restoration was low with no tree species and 2 seedling species per sample plot (0.05 ha). By 2005 restoration areas had an average of 3 tree and 3 seedling species per sample plot, increasing to 5 tree and 9 seedling species per plot in 2013. However, biodiversity was still significantly lower than old-growth forest, at 8 tree and 16 seedling species in an equivalent area. The results suggest that forest restoration is beneficial for AGB accumulation with planted stems storing the majority of AGB. Changes in biodiversity appear slower; possibly due to low stem turnover. Overall this restoration treatment is an effective means of restoring degraded land in the area, as can be seen from the lack of regeneration in degraded plots, which remain low-AGB and diversity, largely due to the impacts of fire and competition with grasses.

4.2. Introduction

Large areas of forest lands have been converted to other land uses, and large areas of degraded tropical forest exists, covering some 550 million ha by some estimates (Pan et al., 2011). Degraded forests and abandoned agricultural lands have the potential to recover back to higher carbon and biodiversity value forest if left to regenerate naturally. However, natural regeneration is often arrested in very heavily degraded lands (Paul et al., 2004, Lawes and Chapman, 2006). One of the major factors leading to arrested succession is the increased susceptibility of degraded forest to wildfires (Cochrane, 2003). In addition, other factors can exacerbate arrested succession in degraded areas. Seed banks are often poor following logging or agricultural cultivation, due to topsoil removal (Dupuy and Chazdon, 1998). Seed rain from surrounding forest into degraded land can also be limited, with wind dispersed seeds often not travelling large distances (Cubina and Aide, 2001) and animal dispersed seeds rarely found, as few forest animals pass through such areas (Holl, 1999). Thus, the distance to the nearest primary forest can determine the success of regeneration (Cubiña and Aide, 2001). This is problematic in highly fragmented habitats where only small patches of forest remain, particularly if the species composition of such fragments is not representative of old-growth forest.

Thus, large areas of abandoned degraded land, and their propensity for arrested succession, mean that forest restoration could play a vital role in mitigating climate change. Not only could restored forest sequester carbon, they also have the potential to aid the recovery of biodiversity and ecosystem function. Collectively these factors have increased the desirability of forest restoration, often termed Forest Landscape Restoration (Chazdon et al., 2016a).

Despite active management to restore forests being suggested as a potentially important method to increase terrestrial carbon storage and improve ecosystem function of tropical forests, research is sparse. In particular, very little is known about the long-term effects of forest restoration in terms of forest structure, carbon sequestration, and changes in biodiversity. This evidence is necessary as, the costs associated with forest restoration can be considerable (Lamb et al., 2005). For example, a study by Parrotta and Knowles (1999) estimated that restoration of a bauxite mine in the Amazon cost is $2,500 per ha. Thus, it is

important to quantify the benefits of active forest restoration to ensure restoration projects are successful enough in terms of the long-term recovery of ecosystem services to warrant the costs.

To begin to address this gap in current knowledge, I undertook research in the UWA-FACE (Uganda Wildlife Authority and FACE the future foundation) rehabilitation project, in Kibale National Park, Uganda (hereafter Kibale). Since 1995 this project has been restoring abandoned agricultural land that had become dominated by invasive elephant grass (*Pennisetum purpureum*), due to repeated wildfires (UWA-FACE, 2011). Restoration activities involved protection from fire and replanting with native tree species to restore forest ecosystem functions, and enhancing biodiversity conservation (UWA-FACE, 2007, UWA-FACE, 2011). In 2005 a study was conducted by Omeja et al. (2011a) to assess AGB and biodiversity of the project 10 years after planting.

My aims in this study are two-fold. Firstly, to quantify the effect of tree planting and fire management on AGB accumulation and plant species diversity over 18 years by remeasuring the study plots established in 2005. It is likely that the rate of AGB accumulation will change with increasing time after planting, as has been demonstrated in an Australian tropical forest restoration project (Paul et al., 2015). Specifically, I predict that initial AGB accumulation will be slow as planted seedlings have few photosynthesising leaves, limiting growth, which will increase as the size of trees in the stand increases. Thus, I expect more recent AGB accumulation rates to be greater, and be more representative of rates over the coming decades.

Secondly, I estimate woody plant species diversity after 18 years of restoration. I expect that restoration activities will result in an increase in tree species diversity. Initially tree diversity will be dominated by planted tree species. However, the presence of planted trees is expected to assist natural regeneration and the shade created once a canopy develops will create more favourable conditions for seedlings of old-growth forest species to become established. Furthermore, the presence of planted trees will also encourage the movement of animals through the area and they will bring with them seeds of animal-dispersed species. Therefore, restoration will help increase tree diversity from pre-restoration levels, yet, it is likely to take longer for species composition to become similar to old-growth forest that forest structure of AGB due to the time delay in pioneer planted tree species being superseded by old-growth forest species.

Here, I calculate changes in forest structure, AGB and biodiversity at two periods following forest restoration, 10 years post planting in 2005 and 18 years post planting in 2013, in Kibale National Park and compare these to nearby grassland areas that have not been restored and old-growth forest that has not been degraded.

4.3. Methods

4.3.1. Study Site

This study was conducted in the southern part of Kibale National Park, Uganda (E 30.31 – 30.36, N 0.31 – 0.56, Figure 19). Kibale is a moist evergreen forest covering 795 km^2. It received on average 1672 mm y^{-1} of rainfall between 1992 and 2013 (the project duration). Rainfall distribution is bi-modal with two pronounced rainy seasons, the short rains March–May and the long rains August–November. The park elevation is 1100 – 1500 m.a.s.l., decreasing from north to south, which accompanies a decrease in rainfall and increase in temperature (Struhsaker, 1997).

Kibale has had some form of protection since 1932 (Osmaston, 1959, Baranga, 1991, Struhsaker, 1997), however, during the 1970's and 1980's illegal agricultural encroachment and deforestation took place in the southern part of the park (Chapman and Lambert, 2000), with ~90% of this area having undergone some form of encroachment by the 1990's (Baranga, 1991, Van Orsdol, 1986), predominantly for growing subsistence crops including banana (*Musa* spp), cassava (*Manihot esculenta*) and maize (*Zea mays*) and the removal of timber for fuel wood (Chapman and Lambert, 2000). In 1993, the area that now forms Kibale was given national park status. An estimated 10,000-40,000 people living in the southern part of the park at this time were resettled outside the park boundary (Baranga, 1991, Van Orsdol, 1986, Chapman and Lambert, 2000).

The southern part of Kibale quickly became dominated by elephant grass (*Pennisetum purpureum*), due to repeated fires spreading from nearby subsistence farms or being set by poachers. Elephant grass can grow up to 5 m tall, severly inhibiting natural regeneration of native forest (UWA-FACE, 2011). In 1995 the UWA-FACE Natural High Forest Rehabilitation Project was initiated, a joint forest restoration project between the Uganda Wildlife Authority and FACE the Future, an independent Dutch organization that aims to mitigate climate change via sustainable forest management. The project aimed to replant of 10,000 ha of degraded habitat with native tree species, to improve biodiversity and ecological functions, whilst also producing carbon credits established via monitoring and verification of the replanted areas. By mid-2014 some 3,500 ha had been replanted.

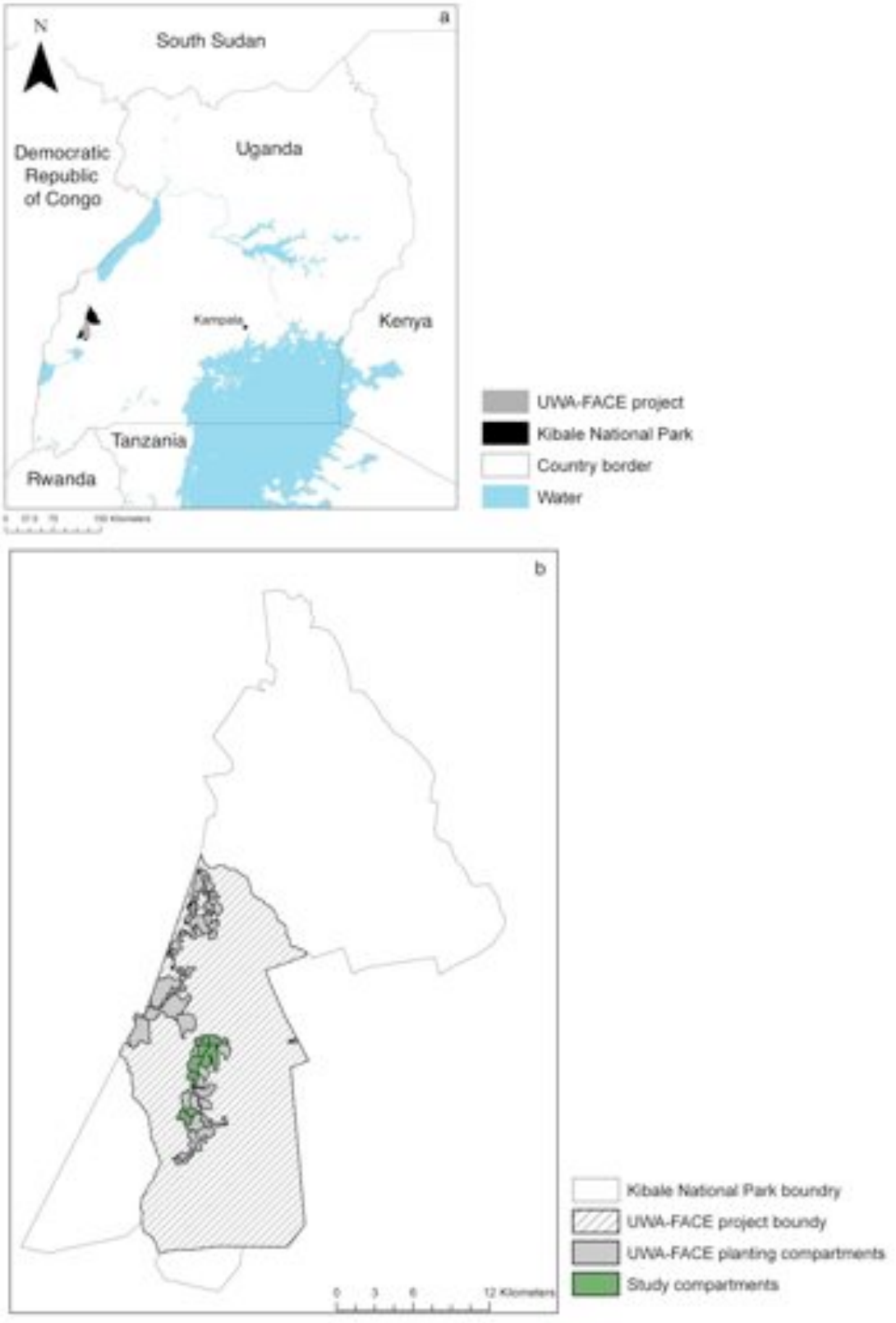

Figure 19. Map showing location of a) Kibale National Park within Uganda, and b) the location of the UWA-FACE project area within Kibale and the planted areas (compartments). Planted areas shown in grey, planted areas measured in this study shown in green.

4.3.2. Forest Restoration

Restoration consisted of protection from fire (creation and maintenance of 10 m fire breaks; staffed fire towers for monitoring) and planting areas with native seedlings (400 ha^{-1}). Seedlings were collected from surrounding forest and raised in a nursery, under partial shade, using local forest soil, without the addition of fertilizer (UWA-FACE, 2011). Seedlings of 0.35 to 1 m tall were planted every 5 m in a grid, unless an existing natural regenerating seedling occurred, when no seedling was planted (of the 400 planting locations per ha, ~30, or 7.5%, had an existing natural regeneration). Prior to planting elephant grasses were cut at ground level in 2 m wide planting lines to reduce competition. For five years following planting, any grasses regrowing along planting lines were cut quarterly, until planted stems were >2 m tall. After five years planted areas were left unmanaged, with the exception that fires were excluded.

All areas monitored in this study were located in the phase one area, which was the first area to be planted, between 1995 and 1997. Thirty-nine species of native tree were planted; the most common were *Markhamia platycalyx (Bignoniaceae), Uvariopsis congensis (Annonaceae), Prunus africana (Rosaceae), Lovoa brownii (Meliaceae),* and *Mimusops bagshawei (Sapotaceae*; see Appendix 2 and Appendix 3 for full list of species planted per compartment and planted species observed in 2013 within sample plots).

4.3.3. Plot-based Sample Design

4.3.3.1.Sample plots

In 2005, ten years after planting, 65 plots (10 x 50 m, 3.25 ha) were established and measured by two of the researchers on the project reported in Omeja *et al.* (2011). Between 27th August and 8th December 2013, I remeasured 50 of these plots (2.5 ha), to assess changes over 18 years. No sampled plots underwent burning since restoration in 1995. Here I reanalyse the 2005 census data (Omeja et al. (2011a) and the new 2013 census data.

I also measured 20 plots (10 x 50 m, Total = 1 ha), across Kibale in old-growth forest to make comparisons with restoration forest. Old-growth plots were located in existing

permanent sample plots (established by C. Chapman in 1989). A further six plots were established in grassland within the UWA-FACE project boundary. This area was originally forest, and underwent the same disturbance as restoration areas, however since abandonment in 1992 it has yet to receive any management. Therefore, I consider it representative of the area immediately before planting. Within this areas grassland plots were located at random but a minimum of 100 m from the grassland edge and each plot was separated by a minimum distance of 300 m.

4.3.3.2.Sampling within plots

Within each 0.05 ha plot area all stems ≥10 cm DHB (diameter at breast height) I recorded: DBH, species, height, location, and whether the stem was planted or naturally regenerating. DBH was measured at 1.3 m along the stem, except in the case of buttress roots or deformities, which were measured 50 cm above the buttress or 2 cm below the deformity respectively (Phillips et al., 2009a). The height of every individual was measured using a handheld clinometer. Individuals were identified to species level were possible. In 2013, all stems >1 and <10 cm DBH were measured in three 5 x 5 m subplots (Figure 20), recording DBH, height, and species for each individual. This data was not collected in 2005. In both 2005 and 2013 ten 1 x 1 m subplots were established through the centre of the plot at 5 m intervals for the sampling of seedlings and saplings (Figure 20). Every seedling (i.e. < 1 m tall) and sapling (1-1.99 m tall) was identified to species and the height recorded. Additionally, the percentage cover of grasses, shrubs, seedlings, and bare ground within each 1 m^2 subplot was estimated and dominant species identified The mortality of planted stems between 1995 and 2013, was calculated (Sheil and May, 1996) as;

$$\text{Mortality } (\lambda) = \frac{\text{Ln}(\text{Stems } T_0) - \text{Ln}(\text{Stems } T_2)}{\text{Time (years)}}$$

Where λ = Instantaneous rate of change (i.e., Percentage mortality per year), T_0 = Number of trees at time 0 and T_2 = Number of trees at second time interval. In each of the six grassland plots three 1 m^2 samples of grasses were collected (Figure 20), dried to constant mass and weighed to obtain the baseline above ground biomass of grasses prior to planting.

4.3.3.3.Leaf Area Index

Hemispherical photographs were taken at 10 m intervals along the centre of the plot (n=6, Figure 20) to estimate leaf area index (LAI) and percentage canopy cover (8 mm F3.5 EX DG Fisheye Sigma lens; Canon 350d SLR camera; CAN-EYE V6.1 software). All six photographs from a single plot were processed together producing a mean LAI per plot, using an angular resolution of 2.5° in both Zenith (θ) and Azimuth (φ) directions. A view zenith angle of 0° - 60° was selected as it is a high enough resolution to extract canopy gaps of <6 cm (Leblanc et al., 2005), whilst also removing the extreme edges of the images that are dominated by woody material such as trunks so not required for LAI estimation. No hemispherical photographs were taken in 2005.

4.3.3.4.Soil

Four, 30 cm deep, soil cores were taken in each plot at 10 m, 20 m, 30 m and 40 m (Figure 20) using a handheld Edjilcamp soil corer with a 26 mm diameter. Cores were sampled at four depths (0-5 cm, 5-10 cm, 10-20 cm and 20-30 cm). Soil colour was determined using a Munsell soil colour chart. The physical and chemical properties of soil samples were analysed to determine the structural stability and fertility of soils in the restoration and old-growth forest. No soil cores were in 2005, therefore comparisons of soil properties can only be conducted between restoration plots in 2013 and old-growth forest plots.

The proportion of sand, silt, and clay in samples was analysed to determine the physical soil properties using the method outlined in Van Reeuwijk (2002). Also, pH of soil was determined following the methods described in Van Reeuwijk (2002). Carbon and Nitrogen percentage were determined using a gas combustion analyser. Total extractable phosphorus was analysed using a sequential extraction technique as described in Tiessen and Moir (1993). Finally, a modified Silver Thiourea method(Dohrmann, 2006) was used to analyse Cation Exchange Capacity and effective Cation Exchange Capacity (eCEC) was calculated as:

$$eCEC\ (mmol^{+}\ kg^{-1}) = \Sigma\ [Al^{3+}] + [Ca^{2+}] + [K^{+}] + [Mg^{2+}] + [Na^{+}]$$

For a full explanation of soil analysis methods see Quesada et al. (2010). Principal Component Analysis (PCA) was used to reduce 12 structural variables (3 x Sand, silt and clay at 4 x depths) into two principal components that explained 90% of variation in the data. Soil chemical properties in old-growth forest and restoration forest in 2013 were compared using unpaired T tests and Holm sequential Bonferroni correction (Holm, 1979) to account for multiple comparisons.

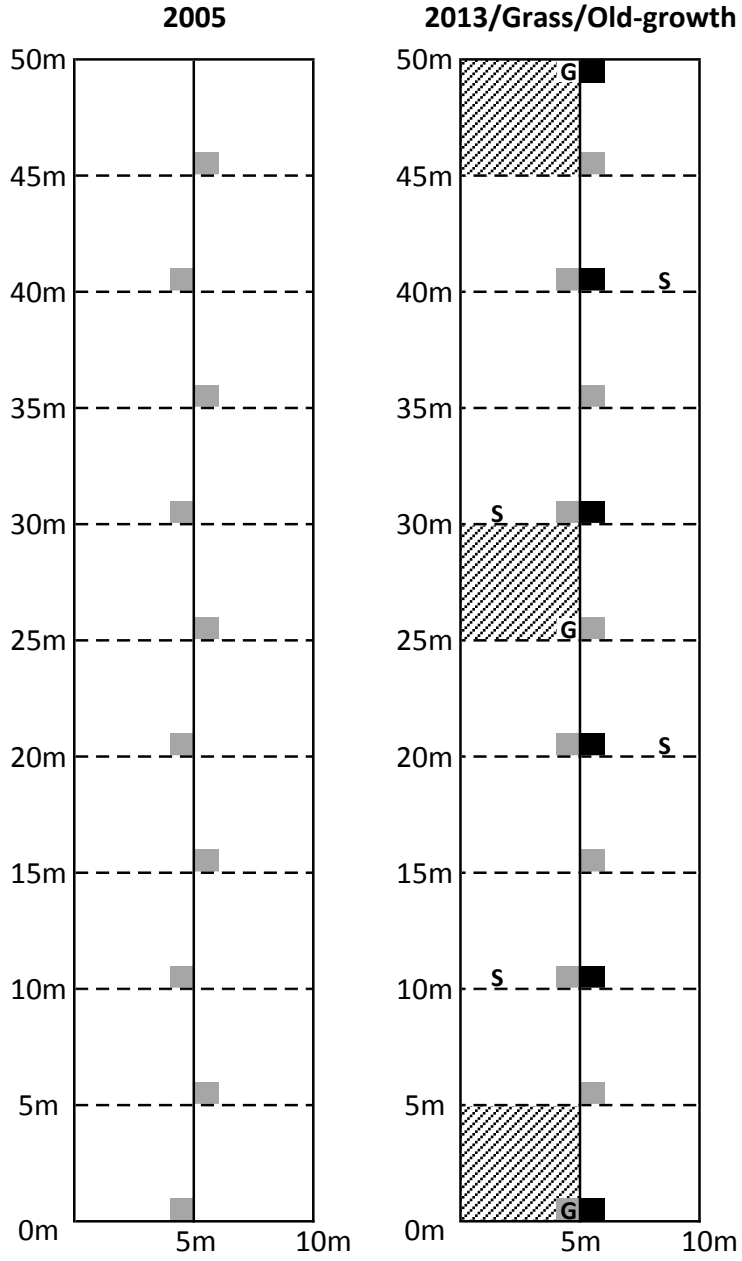

Figure 20. Sample plot layout in restoration forest (2005, Left) and in restoration forest (2013), grassland and old-growth forest (Right). Trees ≥10 cm DBH measured across 10x50 m plot, grey hashed area = trees 1<10 m DBH measured, grey shaded area = Seedlings, % ground cover measured. Black area = hemispherical photograph point,, G = grass sampling point (grassland plots only).

4.3.4. Data Analysis

4.3.4.1.Biomass and height

See section 2.2.1.1 for explanation of AGB calculations. Species-specific wood densities (WD) were available for 78 species, genus mean WD for 32 species and familial mean WD for 5 species. Family was unknown for five individuals therefore the mean plot WD was used (see Appendix 4. for full species list).

Two structural parameters were analysed: First, the stand-level asymptotic maximum height of trees in all plots was determined using non-linear regression and AIC was used to compare models. A two-parameter aysmptotic model of the form: $y = a\ (1 - \exp^{(-bx)})$, was found to be the best fit to the data for all three habitats; 1) restoration forest in 2005 2) restoration forest in 2013 and 3) old-growth forest). Secondly, I analysed the size frequency distribution of stems using doubling size classes (1-2 cm, 2-4cm…..64-128 cm) to account for the exponential decrease in stems as DBH increases, with the expectation that old-growth forest will exhibit an inverse-J shaped distribution (Kohyama, 1986). Additionally, I assess the wood density of trees. Wood density (WD) is a readily available plant species trait that is correlated with growth and mortality and has been related to shade tolerance of tropical forest species (Whitmore, 1998, Philipson et al., 2014). In the high light environment of the restoraiton area, shade tolerance is likely to be an important factor in determining the survival of planted species, therefore we compare the WD of species that were planted, survived and died using ANOVA.

4.3.4.2. Tree diversity and species composition

See section 2.2.1.2 for explanation of diversity and species composition analysis.

4.4. Results

4.4.1. Forest Structure and Biomass

4.4.1.1. Grassland

In grassland plots, which were representative of the area prior to restoration, there were no trees ≥10 cm DBH. Total AGB was 5.1 Mg ha^{-1} (± 1, 95% CI), of which 4.1 Mg ha^{-1} (80%) was elephant grass and 1 Mg ha^{-1} was saplings <10 cm DBH. Grasses dominated ground cover (66% ±5), with some shrubs (15%, ±4) and very low seedlings cover of 1% (±0.6). Stems between 1 and 10 cm DBH had a density of 1,733 (± 1,341), and BA of 0.8 m^2 ha^{-1} (± 0.6). Canopy cover was low at 20% (± 10), with an LAI of 1.4 (± 0.5).

4.4.1.2. Replanted forest 10 years after planting

In the restoration area, ten years after planting (in 2005) the density of stems ≥10 cm DBH had increased to 130 stems ha^{-1} (± 21), with an AGB of 9.5 Mg ha^{-1} (± 2.9), a basal area of 2.4 m^2 ha^{-1} (± 0.5), and a wood density of 0.57 g cm^3 (± 0.02). With most stems and AGB being found in the 8-16 cm size class (Figure 21). The canopy was still relatively short with an asymptotic canopy height of 11 m (± 0.6). The percentage cover of grasses had more than halved in the ten years since planting to 31% (± 2), with elephant grass (*P. purpureum*) still being the most common species, found in 35% of plots. Meanwhile shrub ground cover doubled to 32% (± 2) with *Lantana camera* being the most common shrub found in 36% of plots. Seedling cover increased five-fold to 5% (± 1).

4.4.1.3. Replanted forest 18 years after planting

In the second census of the restoration plots in 2013, stem density (≥10 cm DBH) and BA increased significantly to 349 stems ha^{-1} (± 43) and 8.8 m^2 ha^{-1} (± 1.4), respectively (Stems p = <0.001, BA p = <0.001). AGB increased by 29 Mg ha^{-1} to 40.6 Mg ha^{-1} (± 7.7), but not significantly so. There was no change in wood density (0.57 g cm^3 ± 0.01). Whilst there were more stems between 8 and 16 cm DBH, ~50% of AGB was stored in stems between

16 and 32 cm DBH (Figure 21). Asymptotic canopy height had increased to 15 m (± 1). The addition of stems between 1 and 10 cm DBH added a further 8,358 stems ha^{-1} (± 2,880), 10 Mg ha^{-1} (± 1.5) AGB, and 5.4 m^2 ha^{-1} (± 0.7) of BA.

The percentage cover of grasses had decreased further to 19% (± 2). More importantly, the species composition of grasses changed dramatically, with an unidentified species, local name Panicum, becoming the most common species, found in 41% of plots whereas, elephant grass was found in just 4% of plots. Panicum appears not to compete so effectively with seedlings and saplings, growing to a maximum of 10 cm, and was also present in 12% of old-growth forest plots. Shrub cover increased to 44% (± 3), dominated by the invasive species *L. camara*. There was no change in seedling cover. In the 18 years since planting, canopy cover increased considerably from 20% to 73% (± 5), with an LAI of 4.5 (± 0.3).

4.4.1.4.Old-growth forest

In old-growth forest stem density (≥10 cm DBH,) was not significantly greater than seen in restoration plots in 2013 ($p = 0.13$), at 413 stems ha^{-1} (± 66). However, AGB, BA and wood density were all significantly larger than in restoration forest at 415 Mg ha^{-1} (± 111, $p = <0.001$), 34 m^2 ha^{-1} (± 5, $p = <0.001$), and 0.62 g cm^3 (± 0.02, $p = 0.003$), respectively. The frequency distribution of stems is a typical inverse-J shape (Figure 21). There is a much higher density of stems >32 cm DBH compared to restoration forest after 18 years, with 85% of AGB found in stems ≥32 cm DBH and 55% of AGB in stems ≥64cm DBH (Figure 21). Asymptotic canopy height is also taller in old-growth forest at 47 m (± 5). Stems between 1 and 10 cm DBH comprise 6,400 ha^{-1} (± 2,211), 12.6 Mg ha^{-1} (± 2.9) of AGB and 4.9 m^2 ha^{-1} (± 0.9) of BA. The percentage cover of grasses and shrubs was the same (22% ± 3), however, seedling cover was higher than seen in restoration forest (12% ± 1). Old-growth forest canopy cover and LAI were both higher than seen in restoration forest (92% ± 2.7; LAI = 6.3 ± 0.2).

4.4.1.5.Biomass Accumulation

Eighteen years after planting the AGB of restoration forest equates to 12% of old-growth AGB. The initial net AGB accumulation rate during the first ten years after planting of

stems ≥10 cm DBH was slow, at 0.95 Mg ha^{-1} yr^{-1}. However, between 10 and 18 years after planting AGB accumulation increased to 3.9 Mg ha^{-1} yr^{-1}. If AGB accumulation continued at 3.9 Mg ha^{-1} yr^{-1} it would take a further 96 years for restoration forest to attain old-growth forest AGB (i.e. a total of 114 years).

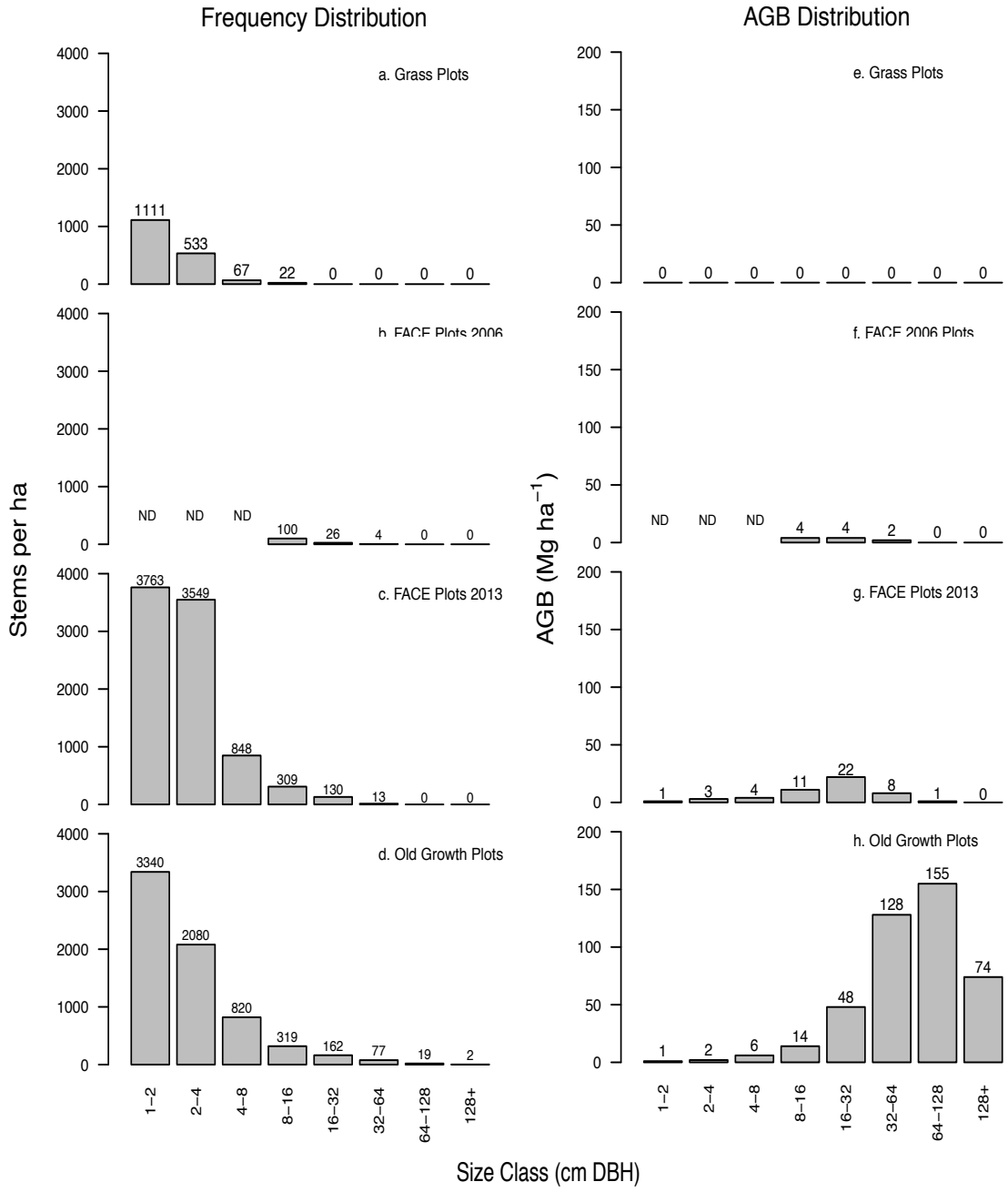

Figure 21. Size frequency distribution for all size classes in a. Grassland, b. Restoration plots 2005 c. Restoration plots 2013 and d. Old-growth forest plots, and above ground biomass distribution for trees ≥ 1 cm DBH in e. Grassland, f. FACE plots 2005, g. FACE plots 2013 and h. Old-growth forest plots. ND = no data available (Data presented for FACE plots in 2005 is only for stems ≥10 cm DBH).

4.4.1.6.Biomass Accumulation and forest structure of Planted verses Non-Planted Trees.

In the sample plots in 1995, an average of 390 stems ha^{-1} (± 20) were planted with an additional 30 naturally regenerating stems ha^{-1} (± 12) located at planting positions that received management, combined this is slightly higher than the 400 ha^{-1} expected. Planted stems had an annual mortality of 3%, leaving 153 planted stems ha^{-1} (± 20) in 2013. In 2005, just 33% of AGB and 37% of BA of stems >10 cm was stored in planted stems, despite 50% of stems being planted (Table 16). By 2013, the majority of stems >10 cm were planted individuals (61%), and most AGB (69%) and BA (66%) was stored in planted stems (Table 16). Wood density of planted and non-planted stems was not significantly different in either census (2005; T = -1.04, df = 66.2, p = 0.3, 2013; T = -1.9, df = 95, p = 0.07), with planted stems having slightly higher WD (Table 16). The recruitment of planted stems ≥10 cm was almost double that of non-planted stems (T = 2.6, df = 98, p = 0.009), and AGB accumulation rate of planted stems was significantly higher than seen in non-planted stems (T = 6.2, df = 71, p = <0.001; Table 16). Thus, it appears that the planted stems are becoming increasingly dominant as the forest matures.

Table 16. Total AGB, BA and stem density for planted and non-planted trees ≥10 cm DBH in 2005 and 2013. Accumulation rate for planted and non-planted stems between 2005 and 2013. 95% CI in Parentheses.

		2005	2013	Accumulation ($year^{-1}$)
Above Ground Biomass ($Mg\ ha^{-1}$)	Planted	3.3 (1.1)	28.2 (5.6)	3.1 (0.7)
	Non-Planted	6.6 (2.9)	12.4 (3.3	0.7 (0.3)
Basal Area ($m^2\ ha^{-1}$)	Planted	0.9 (0.2)	5.8 (1)	0.6 (0.1)
	Non-Planted	1.5 (0.5)	3 (0.6)	0.2 (0.1)
Stem Density (≥10 cm DBH ha^{-1})	Planted	62 (12)	215 (34)	19 (4)
	Non-Planted	61 (15)	135 (34)	9 (4)
Wood Density ($g\ cm^3$)	Planted	0.59 (0.02)	0.58 (0.02)	
	Non-Planted	0.56 (0.04)	0.56 (0.02)	

4.4.2. Biomass and structure of different planted tree species

In 1995 a total of 39 species were planted, which have a mean WD of 0.60 g cm^3 (± 0.01). The most common species, which each constituted >10% of originally planted stems were; *U. congensis, M. lutea, M. bagshawei* and *P. africana* (Table 17). These dominant planted species had a mean WD of 0.61 g cm^3 (± 0.1). Eighteen years after planting, within the area sampled, these same four species each made up <5% of surviving planted stems (Table 17), with just two individuals of *U. congensis*, seven *M. lutea*, 12 *M. bagshawei,* and 17 *P. africana* being observed. Despite only a small proportion of the planted area being sampled, this low encounter rate of the most commonly planted species suggests they have a poor survival rate.

Ten years after planting, in 2005, seven species of planted tree ≥10 cm DBH were observed, of these just three (*B. micrantha, W. ugandensis,* and *S. ellipticum*) made up >95% of planted stem density, AGB and BA (Table 18). Thus, these species have good survival rates. By 2013 an additional eight species of planted tree ≥10 cm DBH were observed, with the same three species still dominating (Table 18). By 2013, *B. micrantha* was by far the most common planted species, making up 62% of planted stems, however it contributed just 33% of AGB (Table 18). This is due to its small size, in terms of mean DBH and height (Table 18). *W. ugandensis*, by contrast contributed 55% of planted AGB, despite making up <30% of planted stems (Table 18), as *W. ugandensis* is a much larger species than *B. micrantha* (Table 18). Of the naturally regenerating stems *S. ellipticum* and *B. micrantha* were the most common species making up 35% and 23% of individuals, respectively. See Appendix 5 for full list of naturally regenerating species.

Within sample plots the WD of planted species that survived until 2013 was 0.57 g cm^3 (±0.2), significantly lower than the WD of originally planted species ($T = 2.8$, $df = 14$, $p = 0.01$). This could suggest that lower WD species, which may favour the higher light conditions found in restoration areas at the time of planting, have better survival. However, the survival and growth of species is liable to change over the coming years as LAI and canopy cover increase, which would favour more shade tolerant species.

Table 17. Mean percentage (± 95% CI) of 15 most commonly planted seedlings, planted in 1995/6 across the whole planting compartment (above line), and the percentage of total stems remaining in 2013 within the sample plot area. Species below line were observed in 2013 but were not in the top 15 most commonly planted species. ◆ = Species planted in 1995/1996 but not observed in 2013. * = Species were naturally regenerating in 1995/1996 that received management of grasses.

	1995/6	**2013**
	% of all seedlings planted	% of all planted trees ≥1 cm DBH
Markhamia platycalyx	15.1 (3.4)	1.5 (2.6)
Uvariopsis congensis	13.7 (5.2)	0.4 (0.5)
Prunus africana	11.6 (5.5)	3.3 (3.2)
Mimusops bagshawei	10.4 (5.7)	3.3 (4.9)
Lovoa brownii	8.7 (4.5)	◆
Chrysophyllum albidum	4.4 (2.4)	◆
Blighia wildmaniana	4.4 (1.6)	0.2 (0.4)
Warburgia ugandensis	4.6 (3.8)	25 (6.4)
Strombosia scheffleri	3.0 (1.4)	◆
Albizia gummifera	2.6 (2.0)	0.3 (0.5)
Bridelia micrantha	2.9 (4.4)	54.4 (14)
Diospyros mespiliformis	3.2 (2.8)	0.6 (1.2)
Antiaris toxicaria	1.7 (1.2)	◆
Spathodea campanulata	1.9 (1.3)	0.4 (0.8)
Pancovia turbinata	1.7 (0.8)	◆
Celtis durandii	1.0 (0.8)	0.2 (0.3)
Tabernaemontana holstii	0.5 (1.1)	1.9 (2.5)
Sapium ellipticum *		6.5 (3.8)
Croton macrostachyus *		1.6 (2.0)
Allophyllus rubifolius *		0.4 (0.7)

Table 18. Mean stem density (ha^{-1}), basal area (M^2 ha^{-1}), AGB (Mg ha^{-1}) and percentage of total for planted species ≥10 cm DBH in 2005 and 2013. Mean DBH and height (per tree) of planted species in 2005 and 2013. 95% CI in parentheses. Only species with ≥ 5 individuals sampled shown.a = *S.ellipticum* were naturally regenerating stems that received management of grasses.

		Stems (per ha)		Basal area (M^2 ha^{-1})		AGB (Mg ha^{-1})		Average DBH (cm)	Average Height (m)
		Mean	%	Mean	%	Mean	%	Mean	Mean
B. micrantha	2005	36 (12)	57.1	0.5 (0.2)	53.7	1.3 (0.8)	46.2	12.3 (0.6)	7.4 (0.6)
	2013	128 (36)	62	2.5 (0.8)	48.1	7.5 (2.7)	33.4	15.1 (0.8)	8.6 (0.6)
W. ugandensis	2005	23 (8)	36.5	0.3 (0.1)	38.1	1.3 (0.5)	44.4	13.2 (0.6)	8.4 (0.4)
	2013	55 (13)	26.7	2.2 (0.6)	41.9	12.9 (3.8)	57.8	21.7 (1.7)	12.1 (0.6)
S. ellipticum[a]	2005	2 (2)	3.2	0.04 (0.04)	4.3	0.1 (0.2)	4.6	15.8 (0.9)	9.2 (1.5)
	2013	11 (7)	5.3	0.3 (0.2)	5.6	1.2 (0.8)	5.2	18.2 (1.4)	10.4 (0.6)
Other	2005	2 (2)	3.2	0.03 (0.03)	3.9	0.1 (0.1)	4.8	14.4 (0.9)	10.3 (0.6)
	2013	12 (8)	6	0.2 (0.1)	4.4	0.8 (0.5)	3.6	22.1 (2.9)	14 (2.1)

4.4.3. Biodiversity and Species composition

Species richness (N_0) was lowest in grassland with no trees ≥10 cm DBH and just two seedling species per 0.05 ha plot. As time after planting increases, so too did biodiversity, with restoration plots in 2013 having two more tree species and six more seedling species per plot than restoration plots in 2005 (Table 19). Nevertheless, by 2013, restoration plots still had significantly fewer tree species ($T = 4.3$, $df = 26$, $p = <0.001$) and seedling species ($T = 5.4$, $df = 22$, $P = <0.001$), than old-growth forest, which had 8 tree and 16 seedling species per plot (Table 19).

Species evenness (N_2) in stems ≥10 cm also increased in restoration plots between 2005 and 2013, but by very little, suggesting that 18 years after planting, a small number of species still dominate (Table 19). Seedling species evenness increases more than that of trees in restoration plots between 2005 and 2013 (Table 19). However, species evenness in restoration plots in 2013 is still significantly lower than in old-growth forest for both trees ($T = 3.6$, $df = 27$, $p = 0.001$) and seedlings ($T = 3.6$, $df = 26$, $p = 0.001$).

Table 19. Hill numbers N_0, and N_2 for Grassland plots, restoration plots 2005, restoration plots 2013 and old-growth plots for trees ≥10 cm DBH and seedlings ≤1 m. Plot = 0.05ha.

		N_0	N_2
	Habitat	Species Richness	Inverse Simpsons *D*
Trees (≥10 cm DBH)	Grass	0	0
	Restoration 2005	2.8	2.3
	Restoration 2013	4.9	2.9
	Old-growth	8.3	4.8
Seedlings (≤1 m)	Grass	1.7	1.4
	Restoration 2005	2.5	1.1
	Restoration 2013	8.5	3.7
	Old-growth	15.8	5.8

NMDS plots showed that the community composition of trees ≥10 cm DBH in restoration forest and old-growth forest differed markedly. There was a clear clustering of sample plots along NMDS axis 1, with restoration forest plots in 2005 and 2013 noticeably overlapping to the left of axis 1 and old-growth forest plots clustered to the right (Figure 22). The mean NMDS scores in restoration forest in 2013 had shifted to the right along NMDS axis 1, which suggests that species composition was becoming more similar to old-growth forest. There was also some clustering of planted species (in black) over restoration forest plots on the left of NMDS axis 1 (Figure 22). There were some planted species that did not overlap with restoration forest plots, notably *U. congensis* (U.con on Figure 22), this is a species that was rarely encountered in restoration forest despite being planted, but was common in old-growth forest.

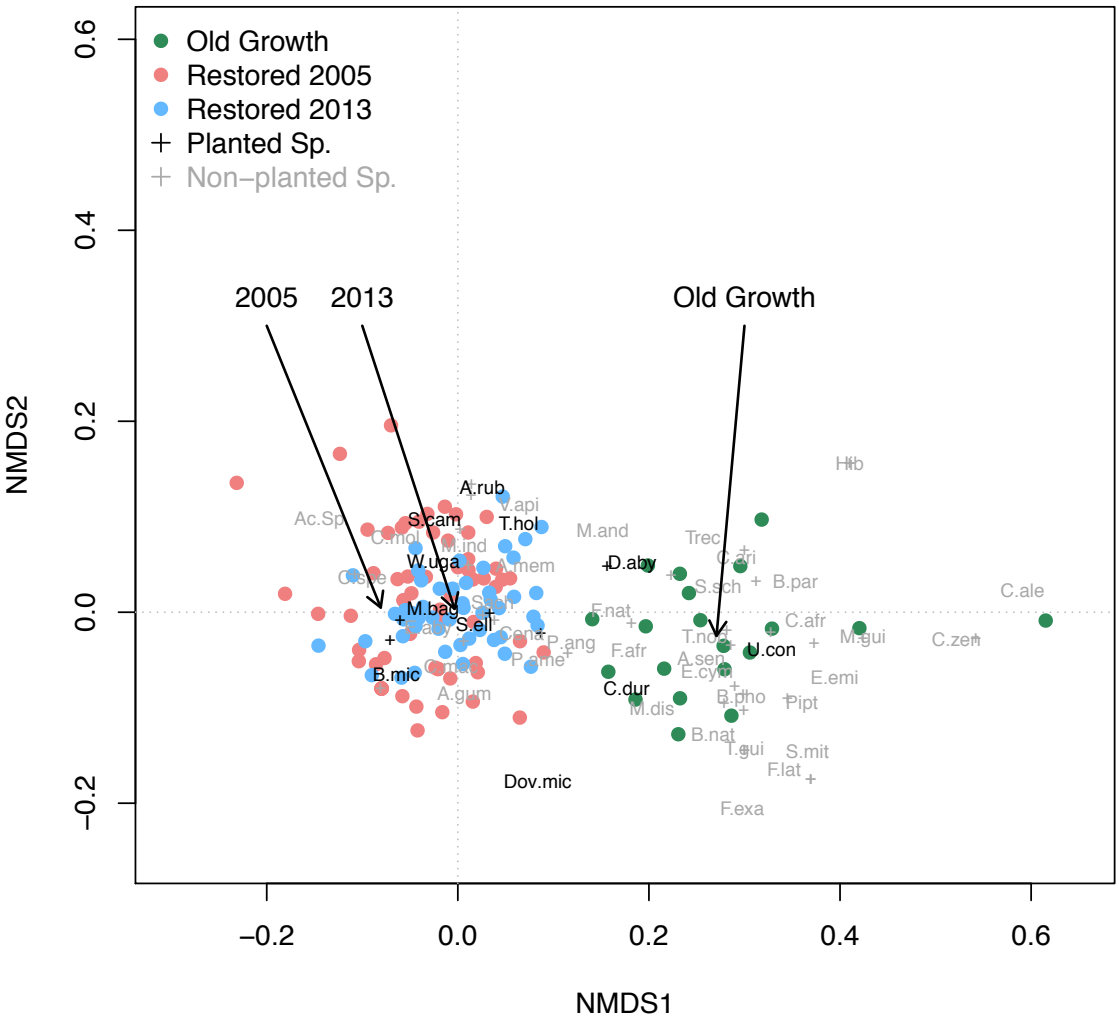

Figure 22. Non-metric multidimensional scaling (NMDS) ordination plot showing community composition of trees ≥10 cm DBH. Species names in black were planted and species names in grey were naturally regenerating (non-planted). Arrows indicate mean NMDS scores for each habitat. Species codes are first letter of genus and first three letters of species name. Species shown; *Acacia Spp., Albizia grandibracteata, Albizia gummifera, Allophyllus rubifolius, Aningeria altissma, Antidesma membranaceum, Baphiopsis parviflora, Bequaertiodendron natalense, Bosqueia phoberos, Bridelia micrantha, Celtis africana, Celtis durandii, Celtis zenkeri, Combretum molle, Craibia* Spp, *Croton macrostachyus, Cynometra alexandri, Dovyalis microcarpa, Ehretia cymosa, Euadenia eminens, Ficus capensis, Ficus exasperate, Funtumia africana, Funtumia latifolia, Gardenia lanciloba, Harrisonia abyssinica, Kigelia moosa, Mangifera indica, Markhamia lutea, Markhamia platycalyx, Mimusops bagshawei, Mintnencea andata, Motandra guineensis, Newtonia buchananil, Piptadeniastrum, Pleiocarpa pycnantha, Premna angolensis, Rauvolfia vomitoria, Sapium ellipticum, Spathodea campanulata, Strombosia scheffleri, Strychnos mitis, Tabernaemontana holstii, Teclea nobilis, Trichilia dregeana, Uvariopsis congensis, Vanguaoria apiculata, Warburgia ugandensis*.

4.4.4. Composition of old-growth and Restoration forest soil properties

A PCA of soil structure produced two principal components that explained 89% of the variation in data. PC1 explained 81.4% of the variation and differentiated between the sand and clay proportion, with high values indicating high clay concentration and low values representing high sand concentration. PC2 explained 7.7% of the variation and corresponded to silt proportion. Variation in soil structure was more variable in old-growth forest plots compared to restoration forest plots. However, PC1 and PC2 were not significantly different between restoration and old-growth forest plots, suggesting that the physical structure of soil was similar between habitats.

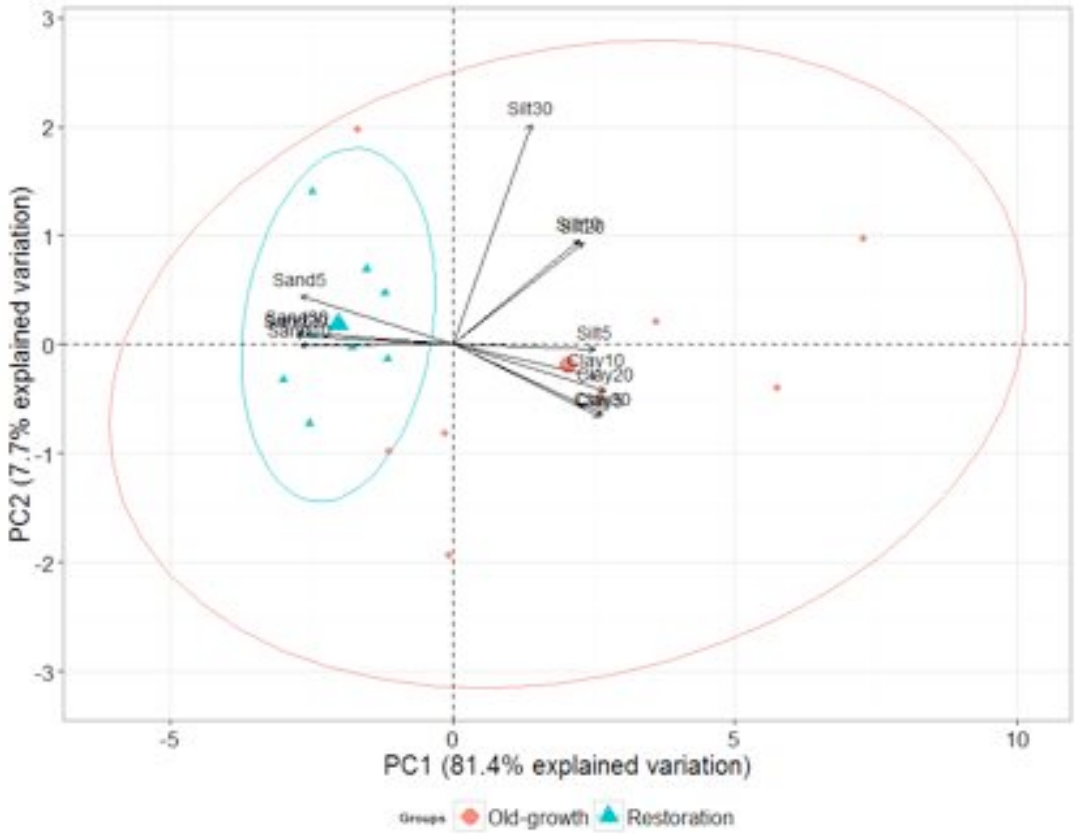

Figure 23. Principal component analysis bi-plot of soil structure (Sand, Silt and Clay) for Restoration and Old-growth plots. Ellipse shows 95% confidence interval around habitat mean value (shown as larger point).

The percentage of Nitrogen in soil was significantly higher in old-growth forest (0.6% ± 0.1) than in restoration forest (0.3% ± <0.1) at 0-5 cm depth, but not at any other depth

(Table 20). Meanwhile, the percentage of Carbon was significantly higher in restoration forest than in old-growth forest at the depths of 5-10, 10-20 and 20-30 cm, but not between 0-5 cm deep (Table 20). The higher carbon percentage in restoration forest led to the C: N ratio being significantly higher on average in restoration forest than in old-growth forest (Table 20), at 13.8 (±0.5) and 9.7 (±0.6), respectively.

Soils in restoration and old-growth forest were slightly acidic, however pH was not significantly different between habitats (Table 20). There was also no significant difference in total extractable P and eCEC (Table 20). The proportion of cations in decreasing order was Ca > Mg > K > Na > Al, making up 57.5 % (± 4.3 %; 34.3 $mmol^{+}\ kg^{-1}$ ± 3.3), 33.0 % (± 1.9 %; 19.7 $mmol^{+}\ kg^{-1}$ ± 1.7), 9.3 %(± 3.0 %; 5.5 $mmol^{+}\ kg^{-1}$ ± 1.6), 0.14 % (± 0.05 %; 0.09 $mmol^{+}\ kg^{-1}$ ± 0.03) and 0.03 % (± 0 %; 0.02 $mmol^{+}\ kg^{-1}$ ± <0.01), respectively.

Table 20. Soil physical and chemical properties in restoration and old-growth forest plots and T test results showing *t* values, degrees of freedom P value and adjusted P value (*a* = Holm) at all depths. Bold values show significantly different results for P and P *adj*. 95% CI in parentheses.

Variable	Depth	Restoration	Old-growth	t	DF	P	P *adj* [a]
PC1 (sand-clay axis)		-2.0 (0.5)	2.0 (2.3)	3.4	7.60	0.01	0.28
PC2 (silt axis)		0.2 (0.5)	-0.2 (0.8)	-0.7	14.00	0.47	1
pH	0 - 5	6.5 (0.2)	6.3 (0.4)	-0.57	8.8	0.58	1.00
	5 - 10	6.1 (0.2)	6.1 (0.4)	-0.26	9.5	0.80	1.00
	10 - 20	5.9 (0.1)	6.1 (0.4)	1.05	9.1	0.32	1.00
	20 - 30	5.8 (0.1)	6.2 (0.3)	2.26	7.3	0.06	0.90
	Mean	6.1 (0.3)	6.2 (0.1)				
N%	0 - 5	0.3 (0.0)	0.6 (0.1)	5.03	7.0	**0.00**	**0.04**
	5 - 10	0.4 (0.0)	0.3 (0.0)	-2.46	14.0	0.03	0.52
	10 - 20	0.3 (0.0)	0.3 (0.0)	-0.64	14.0	0.53	1.00
	20 - 30	0.2 (0.0)	0.2 (0.0)	-1.38	10.1	0.20	1.00
	Mean	0.3 (0.1)	0.3 (0.2)				
C%	0 - 5	5.2 (0.5)	6.5 (1.7)	1.40	8.1	0.20	1.00
	5 - 10	4.2 (0.2)	2.9 (0.4)	-4.99	9.6	**0.001**	**0.02**
	10 - 20	3.7 (0.2)	2.3 (0.4)	-5.89	14.0	**<0.001**	**0.00**
	20 - 30	3.3 (0.3)	1.7 (0.5)	-5.09	14.0	**<0.001**	**0.01**
	Mean	4.1 (0.8)	3.4 (2.1)				
C: N	0 - 5	13.1 (0.7)	10.5 (0.6)	-7.09	14.0	**<0.001**	**<0.001**
	5 - 10	13.8 (0.5)	9.5 (0.6)	-11.51	14.0	**<0.001**	**<0.001**
	10 - 20	13.9 (0.7)	9.0 (0.6)	-10.52	14.0	**<0.001**	**<0.001**
	20 - 30	14.4 (0.3)	9.8 (0.7)	-11.08	9.3	**<0.001**	**<0.001**
	Mean	13.8 (0.5)	9.7 (0.6)				
P (Mg kg^{-1})	0 - 5	1037 (124)	841 (153)	-1.90	13.0	0.08	1.00
	5 - 10	994 (165)	736 (125)	-2.34	13.0	0.04	0.61
	10 - 20	848 (186)	634 (156)	-1.66	13.0	0.12	1.00
	20 - 30	756 (191)	591 (173)	-1.20	13.0	0.25	1.00
	Mean	909 (127)	701 (109)				
eCEC ($mmol^{+}$ kg^{-1})	0 - 5	55.8 (15.3)	72.9 (5.8)	2.05	8.9	0.07	1.00
	5 - 10	62.3 (1.4)	63.2 (8.6)	0.21	6.3	0.84	1.00
	10 - 20	60.3 (1.8)	57.5 (3.0)	-1.68	13.0	0.12	1.00
	20 - 30	59.8 (1.9)	59.1 (3.3)	-0.37	13.0	0.72	1.00
	Mean	59.6 (2.7)	63.2 (6.8)				

4.5. Discussion

4.5.1. Effects of active restoration on above ground biomass and carbon sequestration

This study demonstrates that the effective restoration of this heavily degraded tropical forest site is possible using a combination of management to exclude fire plus tree planting. Above ground biomass accumulation of stems ≥10 cm DBH increased four-fold to 3.9 Mg ha^{-1} $year^{-1}$ between 10 and 18 years, showing significant carbon sequestration. This result shows a danger of relying on short-term studies to predict long-term accumulation of AGB in restoration forest, as early AGB accumulation rates are likely to be unrepresentative of long-term trends. Indeed, using the first 10 y accumulation rate suggests it would take a further 400 years for AGB to reach old-growth levels, whereas we estimate if will take a further 96 years. The initially slow rate of AGB accumulation is likely due to two factors. Firstly, the relatively small numbers of photosynthesizing leaves on small tree seedlings means that growth is slow. Secondly, as dense elephant grass (*P. purpureum*) was removed (~5 Mg ha^{-1}), new growth from seedlings must compensate for this before there is a net AGB increase.

After 18 years restoration forest is still in the early stages of succession therefore it is uncertain how the rate of AGB accumulation will change in the future. However, I could predict that the maximum rate of AGB accumulation would not exceed the rate of above-ground wood production (AGWP) seen in nearby old-growth forest permanent sample plots, of 6.9 Mg dry mass ha^{-1} $year^{-1}$ (±1.2, 95% CI, C. Chapman, unpublished data). AGWP is calculated as the difference in AGB for stems that were present in the first and second census, plus the AGB of any new stems that appeared in the second census (Talbot et al., 2014), i.e. the new additions of woody dry mass into the forest system. Accumulation of AGB is equal to AGWP minus biomass losses due to mortality, therefore maximum AGB accumulation is likely to be lower than AGWP. However, AGWP is still considerably higher than the AGB accumulation rate calculated in this study, suggesting that increases in carbon sequestration in the restoration plots are possible.

Once the restoration forest canopy fully closes the stand will likely start to self-thin, with slower growing, shade tolerant late-successional species beginning to supersede the planted pioneer trees and early successional species (Rees et al., 2001, Finegan, 1996). This will create a more uneven aged stand, mimicking the recruitment and mortality dynamics seen in old-growth forest (Sheil and May, 1996). An increase in mortality will eventually lead to a reduction in overall AGB accumulation rate, at the stand level, as the stand approaches the AGB of old-growth forest (Lichstein et al., 2009).

I know of only three studies that monitored tropical forest restoration treatments for a period greater than 18 years, all from Australia (Catterall et al., 2012, Kanowski et al., 2003, Preece et al., 2012). However, all of these studies were forest chronosequence studies, rather than repeated measurements of permanent sample plots, and only one estimated AGB accumulation (Preece et al., 2012). Therefore, I believe my study is the longest duration study of tropical restoration using repeated sampling. Preece et al. (2012) estimated AGB accumulation of 12 Mg ha^{-1} yr^{-1} in restored forest, much higher than our 3.9 Mg ha^{-1} yr^{-1} estimate. Whilst AGB accumulation rates of over 12 Mg ha^{-1} yr^{-1} have been recorded in the tropics (E.g. Fehse et al., 2002, Hertel et al., 2009), these have generally be located in habitats different to that found in Kibale. For example Fehse et al. (2002) estimated AGB accumulation of 14.2 Mg ha^{-1} yr^{-1} during the first 8 years following logging, however, this was in high altitude (>3000 m) forest in Ecuador. The high AGB accumulation rate estimated by Preece at al. could be a result of AGB accumulation being averaged across three different planting types, which included eucalyptus plantations, mixed timber plantations, and diverse 'ecological' plantations. The inclusion of fast growing eucalyptus plantations may have resulted in a higher accumulation rate that is not representative of biomass accumulation in ecological restoration projects if measured alone.

A recent pair of studies (Martin et al., 2013, Poorter et al., 2016) estimated the time it would take for the AGB of abandoned agricultural land to reach that seen in old-growth forest. In a meta-analysis of 74 studies Martin et al. (2013), found that tropical secondary forest, with no management interventions, reached old-growth forest AGB in an average of 80 years. Meanwhile, in an analysis of 45 neotropical sites, Poorter et al. (2016) estimated it would take 66 years for abandoned agricultural land to attain 90% of old-growth forest

AGB. In both cases this is shorter than the further 96 years estimated in this study for restoration forest to reach old-growth forest AGB. There are a number of possible explanations for this difference. Firstly, the majority of studies used by Martin et al. (2013) and all of the site in Poorter et al. (2016) were from Latin America and therefore may have different climatic conditions to Kibale. Secondly, in Martin *et al.* their definition of secondary forest was 'previously forested land undergoing secondary succession following total or near total removal of trees'. Therefore, some areas may have started with higher initial AGB than the low 5 Mg ha^{-1} at Kibale. Thirdly, Poorter *et al.* excluded sites that were experiencing arrested succession, as was the case in Kibale, and state that this could lead to slight overestimation of recovery rates. Finally, the AGB of old-growth forest may be lower than the 415 Mg ha^{-1} seen in Kibale, as AGB is lower over large areas of Latin America compared to Africa, meaning old-growth levels are attained more quickly (c.f. Amazon and Africa AGB, Baker et al., 2004a, Lewis et al., 2013).

In the 18 years since planting, the 1305 ha in the Phase one planting area (where all restoration plots are located) have sequestered an estimated 24,920 Mg of carbon (Lower and upper confidence interval = 20,198 to 29,643 Mg of carbon. Carbon = 47.1% of AGB, Thomas and Martin, 2012). In subsequent planting phases an additional 1936 ha have been planted (3241 ha planted in total to date). Using the accumulation rates calculated in this study an estimated 47,770 Mg of Carbon has been sequestered by the UWA-FACE project by 2013. If the entire 10,000 ha project area were planted and fully restored to reach old-growth forest levels of aboveground carbon storage, the UWA-FACE project area would sequester ~2 Tg carbon (range 1.5 – 2.5 Tg C, 1 Teragram = 10^{12} = 1 Million Mg). Indeed, 2 Tg C is a minimum estimate as it excludes belowground and necromass carbon pools. In old-growth forest carbon storage in belowground and necromass pools are ~25% and ~13% of aboveground carbon, respectively (Lewis et al., 2009, Deans et al., 1996, Phillips et al., 2008), which would contribute an additional ~0.8 Tg C. This is a first-order estimate, as aboveground to belowground and necromass ratios may differ with forest age and structure. Preece et al. (2015) found an aboveground to belowground ratio of 24% in young ecological restoration forest, planted on abandoned pasture, suggesting that this is a reasonable estimate for belowground carbon stocks in the UWA-FACE project. Over the whole project there is a very large potential store of carbon showing the benefits of active forest restoration in an area of degraded forest affected by arrested succession.

All project activities, which include: preparation of land for planting (~10 person days ha^{-1}); planting seedlings (~7 person days ha^{-1}); management of grasses surrounding planted seedlings (~3 person days ha^{-1}); and maintenance of firebreaks cost ~$1,200 per ha over 5 years (UWA-FACE, 2011). If all 10,000 ha of the project area were fully restored the full project costs would be $12 million. Assuming that the entire project area were accumulating carbon at a rate of 1.85 Mg ha^{-1} yr^{-1} (i.e. 3.9 Mg ha^{-1} yr^{-1} of dry biomass with a carbon content of 47.1% or 18,500 Mg yr^{-1} across the whole project area), for the project to break-even within 20 years, carbon would need to be priced at $32 per tonne (i.e. $12 million/20 years = $600,000 per year to sequester 18,500 Mg C yr^{-1} = $32 per tonne). Of course, including belowground carbon and having a longer duration (>20 years), both lower carbon prices. This shows that allocating relatively high carbon prices are necessary if funding for restoration projects such as this is to become readily available.

4.5.2. Effects of active restoration on biodiversity

These study results also suggest that forest restoration is beneficial for tree biodiversity, with both trees ≥10 cm DBH and seedlings <2 m increasing in species richness and evenness since planting (Table 19). However, biodiversity of trees and seedlings is still significantly lower than old-growth forest (Table 19). Furthermore, restoration and old-growth plot had markedly difference species composition (Figure 4). These results support the hypothesis that forest restoration will improve biodiversity, but species composition will take longer to reach old-growth forest levels than AGB, as early successional pioneers tree species, which make up the majority of planted stems are relatively rarely found in old-growth forest. Species composition will become more similar to that of old-growth forest only after the planted pioneer species are superseded, which usually takes a few decades – the average lifespan of many pioneer species (Rees et al., 2001). This is in accordance with a meta-analysis by Martin et al. (2013) who found that in secondary forest, AGB recovery was more rapid than biodiversity recovery. They estimated that biodiversity would reach old-growth forest levels within 100 years, 20 years longer than for ABG to reach old-growth forest levels. They suggested this was a result of the sensitivity of old-growth forest specialists to human disturbance, coupled with small ranges and populations of old-growth species. However, while forest restoration has often been suggested as an important possible approach to slowing

biodiversity losses (Bekessy and Wintle, 2008), and changes in biodiversity have been well documented in natural regenerating forest (Martin et al., 2013, Barlow et al., 2007), to our knowledge ours if the first study into the effect of active restoration on plant biodiversity. Our study highlights the co-benefits that forest restoration may secure for plant biodiversity and carbon sequestration.

4.5.3. Soil composition in restoration and old-growth forest

The impact of soil fertility and structure on forest AGB, wood density and productivity has been well documented (Quesada et al., 2012, Lewis et al., 2013, Paoli et al., 2008). In this study the soils in restoration and old-growth forest are very similar (Table 20), only differences in the percentage carbon and C: N ratio have significant differences (Table 20). A study of 260 plots in Africa by Lewis et al. (2013), found C:N ratio values of between 8 and 60, just 6 plots had a C:N ratio of >20, with the majority of plots having a C:N ratio of between 8 and 14. Therefore, the C: N ratio of 13.8 and 9.7 seen in restoration and old-growth forest plot, respectively, falls within the normal range of C:N ratio values in African forests, so despite being significantly different they do not represent extreme values for C:N. The C: N ratio has been shown to negatively correlate with total extractable P in parts of the Amazon (Quesada et al., 2010) and Africa (Lewis et al., 2013), with high C: N associated with lower extractable P. However, no significant differences in extractable P, which is important for plant growth, were observed between restoration and old-growth forest plots, which could suggest that differences in C: N ratio are not limiting plant growth. Overall, the similarity of soil in this study site suggests that soil fertility is not the dominant factor influencing the accumulation of AGB in restoration sites.

4.5.4. Necessity of active restoration

Without restoration activities it is likely that natural regeneration in Kibale would be extremely limited. This is evident in grassland plots that were not protected from fire and remain dominated by the grass *P. purpureum* 22 years after farming was abandoned, where AGB is 5.1 Mg ha^{-1}. These grassland areas have undergone a burning regime since abandonment in 1992, similar to that which replanted areas experienced prior to the building of firebreaks and planting. The occasional trees present in grassland were

generally fire resistant species, such as *Erythrina abyssinica*, *Combretum molle,* and *Acacia* spp.

Besides managing fire, the planting of seedlings is important for the restoration of heavily degraded land, as after 18 years, almost 70% of AGB is stored in planted trees. Furthermore, planted stems have a much higher AGB accumulation rate than non-planted stems, at 3.1 Mg ha^{-1} y^{-1} verses 0.7 Mg ha^{-1} y^{-1} (Table 13). It is likely that this higher rate of accumulation results from planted stems being given a competitive advantage over non-planted stems due to the regular removal of surrounding grasses early in the restoration process. This assumption is supported by the growth seen in naturally regenerating seedlings that underwent the same management (cutting of grasses) as planted seedlings. These included *S. ellipticum*, which were not planted, but treated in the same way, when they occurred at planting points, which by 2013 was the third most common tree in the planted stands. This suggests that the tending of seedlings, notably reducing competition with grasses, is an important management intervention. Of course, adopting tending of naturally regenerating seedlings as a management technique is dependent on the abundance of naturally regenerating seedlings in grassland areas, which in this study was only ~30 individuals per ha. Cost may become important, as planting in lines to a standard plan gives easier management and possible economies of scale. However, our findings suggest that management to assist the competitive release of naturally regenerating seedlings deserves further study.

Although it is clear that restoration in this heavily degraded region is essential for recovery of AGB and biodiversity, it is unclear whether the combination of fire protection and replanting is necessary for successful restoration or whether fire protection alone would be a suitable restoration technique. A study by Omeja et al. (2011b) estimated AGB in a 0.5 ha grassland plot that was protected from fire for 32 years, also located within Kibale. They found that after 32 years of natural regeneration, AGB of stems ≥10 cm DBH was 29.9 Mg ha^{-1}, accumulating at a rate of 0.9 Mg $ha^{-1}year^{-1}$. They also observed species richness, of trees ≥10cm DBH, of 24 species per 0.5ha plot. This result suggests that natural regeneration of AGB and biodiversity is possible if areas are just protected from fire. However, AGB accumulation in this fire-only protected area is slower than measured in the UWA-FACE project, with an AGB of 40.6 Mg ha^{-1} after 18 years. If AGB were to continue accumulating at the estimated rate of 3.9 Mg ha^{-1} $year^{-1}$, after 32 years the AGB in

restoration forest could potentially reach 95.2 Mg ha^{-1}, more than triple that seen in areas just protected from fire. While Omeja et al. (2011b) only studied a single 0.5 ha fire protected plot, it suggests that the combination of fire protection, planting, and the regular removal of nearby competitors of these seedlings, accelerate carbon sequestration and biodiversity increases compared to fire protection alone.

4.5.5. Problems with active restoration

After 18 years, only 15 of the 39 species that were originally planted were observed in the 50 sample plots. *B. micrantha* and *W. ugandensis*, were the dominant species in 2013, but made up <5% of originally planted stems. Both are pioneer species rarely seen in old-growth forest (UWA-FACE, 2011, Katende et al., 1995). Conversely, *M. platycalyx, U. congensis, P. africana,* and *M. bagshawei* each constituted >10% of originally planted stems (Table 16), but were rarely encountered in 2013, making up between 0.4% and 3% of planted stems (Table 16). The low encounter rate of commonly planted species demonstrates the importance of selecting species with high seedling survival. Pilot studies to evaluate which survival will be extremely useful in improving future restoration, as noted previously in the literature (e.g. Breugel et al. (2011) in a Brazilian context).

The UWA-FACE project adopted a more-or-less trial and error approach. Early planting regimes were monitored to improve the next round of species selection and planting. In the Phase 1 planting area, where this study was carried out, 39 different species were planted, reduced to 22 in Phase 2 and 3 (1997-2002), 16 in Phase 4 and 5 (2003-2006), and 10 species in Phase 6 (2007 onwards). These 10 species with low mortality and high growth rates are; *B. micrantha (Euphorbiaceae), Cordia africana (Boraginaceae), Cordia mellenii (Boraginaceae), Croton macrostarchys (Euphorbiaceae), Croton megalcarpus (Euphorbiaceae), Ficus natalensis (Moraceae), M. bagshawei, P. africana, Spathodea campanulata (Bigogiaceae)* and *W. ugandensis (Canellaceae*) (UWA-FACE, 2011). This has led to some Phase 2 and 3 areas resembling the 18 year old restoration forest in Phase 1 after only 11-16 years (personal observation).

Possibly the biggest ecological problem that could influence the continuation of the forest restoration, is the invasion of the dense shrub *Lantana camara*, which is the most common

shrub in plots in both 2005 and 2013. Native to South America, *L. camara* is planted in nearby villages as an ornamental shrub. It is an extremely fast growing shrub that forms dense thickets, shading out the forest floor and inhibiting the regeneration of seedlings (Zalucki et al., 2007). Across most of its invasive range the spread of *L. camara* is not considered to be under sufficient control (Zalucki et al., 2007). Mangement of *L. camara* may be required in the future, which may include; slashing of plants at base, burning, uprooting, chemical control with herbicides and biological control using natural predators (Love et al., 2009).

4.6. Conclusion

This study adds to the very limited active forest restoration literature. Just three studies were found that monitored restored forest over 18 years, as has been done in this study. However, these used forest chronosequences, thus no previous studies measure changes in AGB, over a long time period, using repeat censuses of permanent sample plots, as this study does, the most reliable sampling method.

It is clear that protection from fire, planting seedlings, and grass cutting, is a successful restoration method, leading to the recovery of above ground biomass, forest structure and biodiversity. Indeed, active restoration of this site is essential for the recovery of this highly degraded area as ~70% of AGB is stored in planted stems after 18 years. However, restoration is a slow process with ~100 years required for restoration forest to reach old-growth forest levels of AGB. For species composition, the delay is likely to be much longer. Therefore, the continued protection of this area is essential if restoration forest is to reach old-growth forest levels of biodiversity and carbon storage.

The continued monitoring of permanent sample plots into the future is needed to understand the long-term dynamics of recovery in restoration forest. The large increase in AGB accumulation from 0.95 Mg ha^{-1} $year^{-1}$ between 0 and 10 years to 3.9 Mg ha^{-1} $year^{-1}$ between 10 and 18 years demonstrates that short-term studies are not accurate in determining long-term trends in restoration forest. The sizeable carbon sequestration benefits possible, ~2 Tg C if all 10,000 ha were restored and attained old-growth AGB level, from this project supports the idea of ecologically friendly tropical forest restoration under schemes such as REDD+, whilst also offering the co-benefit of biodiversity conservation.

5. Forest Restoration impacts on Carbon Sequestration and Biodiversity: a 15 year study of Selectively Logged Forest in Borneo

5.1. Abstract

Southeast Asian forests receive the highest rates of timber extraction across the tropics, which can lead to slow rates of natural regeneration. Silvicultural management, such as planting seedlings may be needed to restore degraded forest to help assist natural regeneration and replace species that were the target of logging. However, there is little long-term evidence of the impact of restoration on carbon sequestration, forest structure and biodiversity. Here I present data from logged forest that was either restored or naturally regenerating and neighbouring primary forest in Sabah, Borneo. Forest was logged 26 years ago and restored 15 years ago using a combination of climber cutting and planting with dipterocarps (max 330 seedlings ha^{-1}), if no naturally regenerating seedling was present. Forest plots (0.2ha) were established in 2007 in areas categorised as having undergone high, moderate or low intensity logging, half in restored areas, half in control areas. Plots were remeasured in 2010, and 2015. By 2015, for trees ≥10 cm diameter, aboveground biomass (AGB) in restoration forest was 356 Mg ha^{-1} (95% of AGB in primary forest), significantly more than AGB in logged forest, 197 Mg ha^{-1} (53% of AGB in primary forest). Accumulation of AGB was twice as fast in restoration forest (7.8 Mg ha^{-1} yr^{-1}) compared to logged forest (3.5 Mg ha^{-1} yr^{-1}). Tree species richness (≥10 cm DBH) was 48 per plot in restored areas, similar to the 46 species found in primary forest, and significantly higher than the 35 species found in logged forest plots. Nevertheless, species composition of restoration and primary forest was very different. Somewhat surprisingly, very few planted stems were found in restoration forest, suggesting that climber cutting and tending – i.e. reducing competition for naturally regenerating seedlings, are the dominant restoration management intervention that are positively impacting forest recovery.

5.2. Introduction

Southeast Asia lost an average of 2.1 million ha of forest annually between 2000 and 2010 (Achard et al., 2014, Hansen et al., 2013), accounting for 0.27 Pg C yr^{-1} emitted from forests in this region (Achard et al., 2014, Baccini et al., 2012, Saatchi et al., 2011), which equates to 29% of the global carbon emissions across the tropics. The island of Borneo has particularly high rates of deforestation estimated at around 0.5 million ha yr^{-1}, or a loss of 1.3% of forest area annually between 2000 and 2010 (Miettinen et al., 2011). Whilst deforestation is high in Borneo, forest degradation, defined here as a reduction in forest biomass, whilst maintaining sufficient canopy cover to be classified as 'forest' (Putz and Redford, 2010, FAO, 2000), is also widespread.

Over the past 50 years the predominant cause of forest degradation in Southeast Asia has been selective logging (Marsh and Greer, 1992). In the state of Sabah, 25% of total land area (1.8 million ha) was intact forest in 2009, however, a further 21% (1.6 million ha) was degraded (logged once) and 10% (0.7 million ha) was severely degraded (Logged more than once, Bryan et al., 2013). Timber extraction rates in Bornean forests are typically 120 m^3 ha^{-1} (Reynolds et al., 2011), much higher than the <50 m^3 ha^{-1} timber extracted rates in tropical Africa and South America (Martin et al., 2015). Usually, all commercially valuable trees ≥60 cm DBH are harvested (Pinard and Putz, 1996), which typically represents between 8 and 15 trees per hecatre (Fui Yee, 2006, Pinard and Putz, 1996), of the family Dipterocarpaceae (Whitmore, 1984).

Selective logging typically uses high lead cable or tractor extraction methods (Whitmore, 1984). These methods are destructive, with 30-40% of the forest being traversed by tractors (Nussbaum et al., 1995), and ~40% of remaining trees in the stand being fatally damaged (Pinard and Putz, 1996). After the first round of selective logging, forests are usually logged again after 15 to 30 years. The minimum cutting diameter permitted is often reduced to 40 cm DBH in order to meet timber demands (Edwards et al., 2011). Timber yields in the second logging round average 35% of the original timber volume extracted in the first logging round (Putz et al., 2012). This yield reduction decreases profits from logging operations and can increase the financial attraction of conversion to oil palm - *Elaeis guineensis* (Koh and Wilcove, 2008, Fisher et al., 2011). Malaysia has the

second largest area under oil palm cultivation globally, after Indonesia, covering 5.4 million ha in 2014, with 1.5 million ha found in Sabah (Malaysian Palm Oil Board, 2014). And it is estimated that 55% to 59% of Malaysian oil palm expansion has come at the expense of primary or logged forest (Koh and Wilcove, 2008).

Despite selectively logged forest loosing approximately 43% of pre-logging AGB, they still offer greater AGB storage in comparison to other land use options (Pinard and Putz, 1996, Berry et al., 2010). For example, after 18 years selectively logged forest store approximately 177 Mg ha^{-1} AGB, 97 Mg ha^{-1} more than in equivalent aged oil palm plantations, which store 80 Mg ha^{-1} AGB (Morel et al., 2011). Additionally, selectively logged forest can retain high biodiversity. A review by Berry et al. (2010) in Sabah showed that species richness of trees, herbaceous plants, mammals and dung beetles did not decline in logged forest compared to primary forest. Furthermore, birds, butterflies, ants, amphibians and termites only lost <10% of species in logged forest. Only termites and canopy butterflies suffered larger declines, losing 34% and 22% of species, respectively. Furthermore, just 8% (range 0 to 33%) of primary forest species were absent in logged forest across all taxa. These results show that while some losses in species richness do occur in selectively logged forest, they are still important habitats for retaining biodiversity of many primary forest taxa.

Selective logging is by definition highly heterogeneous. This creates a forest matrix of relatively undisturbed areas interspersed with heavily degraded areas, such as, areas near to skid trails, log landings, logging camps and roads (Whitmore, 1984). These heavily degraded areas typically have a very high light environment, which is favourable for the invasion of heliophilic climbing bamboos (*Dinochloa* spp.) and vines (including *Merremia* spp. and *Uncaria* spp.). One study in Sabah found that 75% of remnant tree were infested with vines and bamboo 14 year after selectively logging (Pinard and Putz, 1994). Furthermore, in heavily degraded areas the nutrient-rich topsoil is often removed and the remaining soil is highly compacted, making it harder to for seedlings to germinate (Nussbaum et al., 1995, Hattori et al., 2013). The presence of invasive species that can out-compete native species for resources, coupled with degraded soils can severely impede natural regeneration. This creates a need to undertake active management interventions to help assist regeneration of degraded forest.

However, there is very little evidence showing the effects of active restoration in selectively logged forest and how restoration can affect the rate of forest recovery. To begin to address this gap in current understanding, I undertook research at the INFAPRO (Innoprise-FACE the Future) rainforest rehabilitation project in Sabah, Malaysian Borneo, which is restoring 295 km^2 of selectively logged forest.

After logging once in 1989 a carbon monitoring campaign of INFAPRO and the surrounding selectively logged forest was undertaken in 2007 and repeated in 2010, in order to quantify carbon sequestration. In 2014 - 2015 I re-censused these plots to 1) quantify forest structure and tree diversity in restoration forest in comparison to nearby logged and primary forest 2) to determine the rate of forest recovery in restoration forest compared to logged and primary forest.

5.3. Method

5.3.1. Study site

This study was conducted in the INFAPRO rainforest rehabilitation project (N 4.89 - 5.19, E 117.70 - 117.97) and the 438 km^2 Danum Valley Conservation Area (DVCA, N 4.83 – 5.00, E 117.58 - 117.75), both located within the *ca.* 10,000 km^2 Yayasan Sabah Forest Management Area (YSFMA), in Sabah, North-eastern Borneo (Figure 24). This area has an average temperature of 27˚C (between 1988 and 2012, Figure 25), and receives an average of 2,900 mm of rainfall per year (between 1986 and 2012, Figure 25), with the wettest months being November and December (Climate data from Danum Valley field centre).

The DVCA is primary lowland Dipterocarp forest, so-called because the family Dipterocarpaceae dominates tree flora, which is surrounded by forest selectively logged once between 1981 and 1992. All commercially valuable stems ≥60 cm DBH were felled and extracted using either tractor or high lead techniques (Whitmore, 1984). The INFAPRO project area, adjacent to DVCA, falls within this selectively logged forest but has undergone restoration management interventions. In the study I compare AGB, forest structure and tree diversity between the restoration forest and selectively logged forest in the INFRAPRO region and primary forest in the adjacent DVCA (Figure 24).

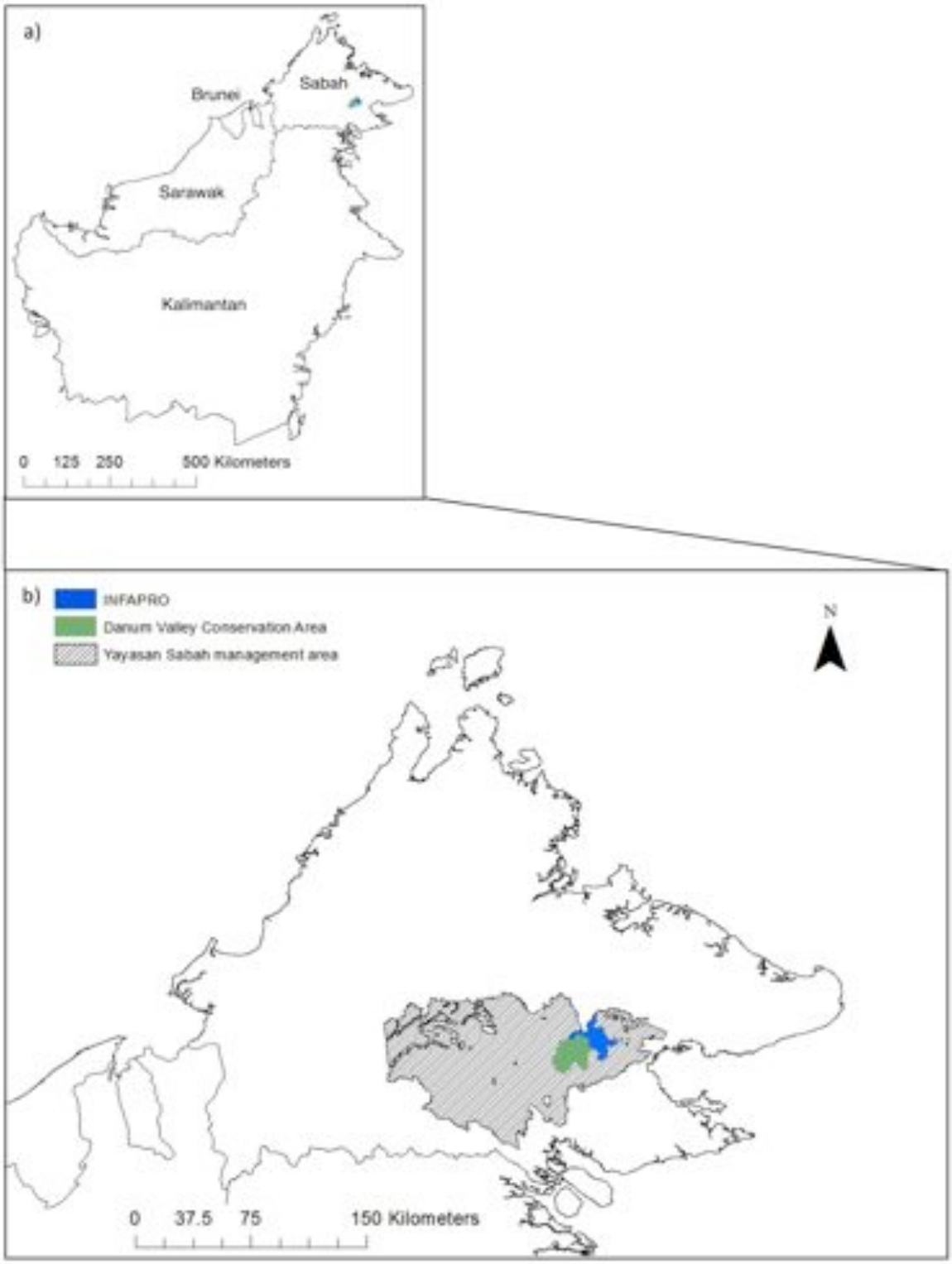

Figure 24. Map of a) Borneo and b) Sabah showing the location of the INFAPRO project and DVCA, within the Yayasan Sabah management area.

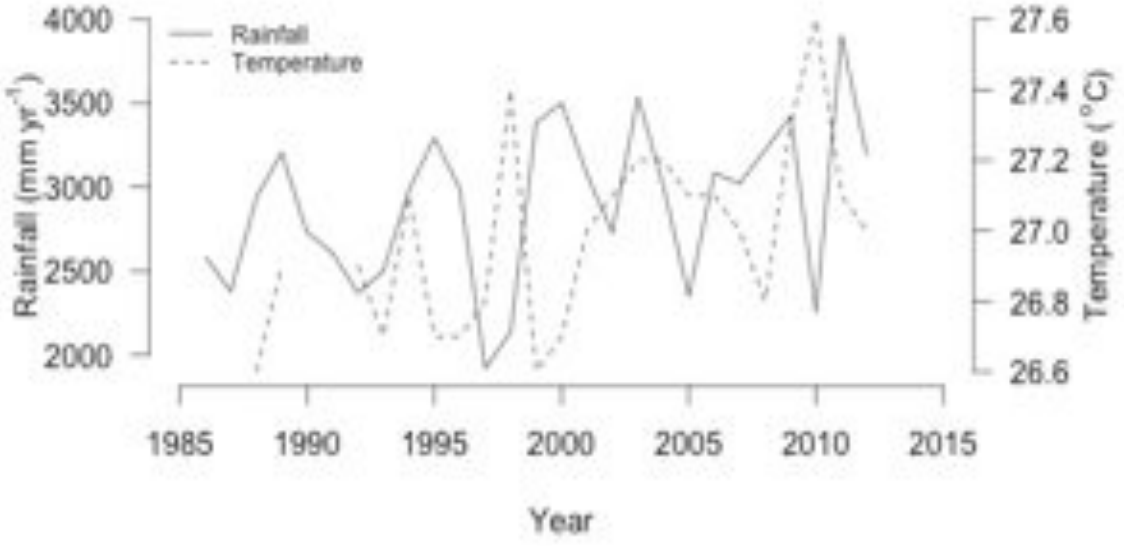

Figure 25. Mean annual rainfall (mm yr^{-1}) and mean annual temperature (^{o}C) at Danum Valley Field Centre between 1986 and 2012. Constructed using data from Danum Valley Field Centre climate station.

5.3.2. Forest Restoration

The forest restoration treatment involved three management actions: cutting all climbing bamboos and vines, enrichment planting with native species and finally, tending of naturally regenerating seedlings (≥1.3 m), found on planting lines.

Management activities were performed as follows: within each compartment all woody vines and climbing bamboos, ≥3 mm diameter, were cut at ground level and at the highest reachable point (~2.5 m) across the entire area. Approximately six months later, 1 m wide planting lines were marked out at 10 m intervals and along these lines any shrubs, herbaceous species or grasses were cut at ground level; naturally regenerating tree seedlings were left uncut. Along each line planting points were marked every 3 m (330 ha^{-1}).

After lines were cut the suitability of each potential planting point was assessed. A planting point was deemed unsuitable for planting if it fell in one of the following; river/stream, swampy or waterlogged area, rocky area, slopes >45˚, beneath the crown of a large standing tree or on skid trails. Additionally, a planting point was also considered unsuitable if there were already two or more naturally regenerating seedlings within 5 m

either side of the planting point. Naturally regenerating seedlings selected were either commercially valuable timber species or species known to attract birds and primates with their fruits. Any shrubs or climbing vines surrounding these seedlings were cut to reduce competition. Following selection these naturally regenerating seedlings were treated identically to planted seedlings. If >10% of planting points in a compartment were suitable for planting then enrichment planting would be conducted.

Seedlings were grown from locally gathered seeds, cultivated in a nursery, and planted at six months old or when they reach a height of 1 m. Approximately 90% of species used for planting were Dipterocarps with the remaining 10% being non-dipterocarps of commercial value and fruit trees (See Appendix 6 for a full list of species planted in each compartment).

'Tending' involved the removal of any unwanted vegetation such as shrubs, vines or climbing bamboo that has regrown along the planting lines. Row slashing was then repeated every three to six months for three years following planting, depending on the conditions of the compartment. In some cases slashing along the entire planting line was not required. In these areas selective ring weeding 0.5 m in radius around seedlings that were surrounded by vegetation was done.

5.3.3. Sample design

Plots were in one of three treatments: (1) primary forest, (2) selectively logged forest, and (3) selectively logged forest followed by restoration treatment. For the selectively logged and restoration treatment plots, 12 permanent-sample plots were selected for each treatment, from a larger number of existing plots. All plots were logged in 1988 or 1989 (Figure 26), and restoration treatments began in 1999 or 2000 (Figure 27). Permanent-sample plots were established in 2007, re-censused in 2010, and re-censused again by me between 8th December 2014 and 13th March 2015. Therefore by census three all plots had been logged 26 to 27 years earlier and restoration plots had been planted between 15 and 16 years earlier. Within the selectively logged and restoration treatments all plots were assessed as having undergone either low, moderate or high intensity logging, based on the criteria detailed in Table 21. A total of four plots were selected per logging intensity level.

Thus, there were 12 replicates of the two main treatments, each split into three levels of initial logging intensity. Each plot was 0.2 ha, and comprised a cluster of four circular subplots, each 500 m^2 in area (Figure 28). Primary forest plots consisted of five, 1 ha plots in the adjacent DVCA (Figure 26 and Figure 27). Three of these were measured in 2006 and again 2013. The remaining two were measured once, in 2013.

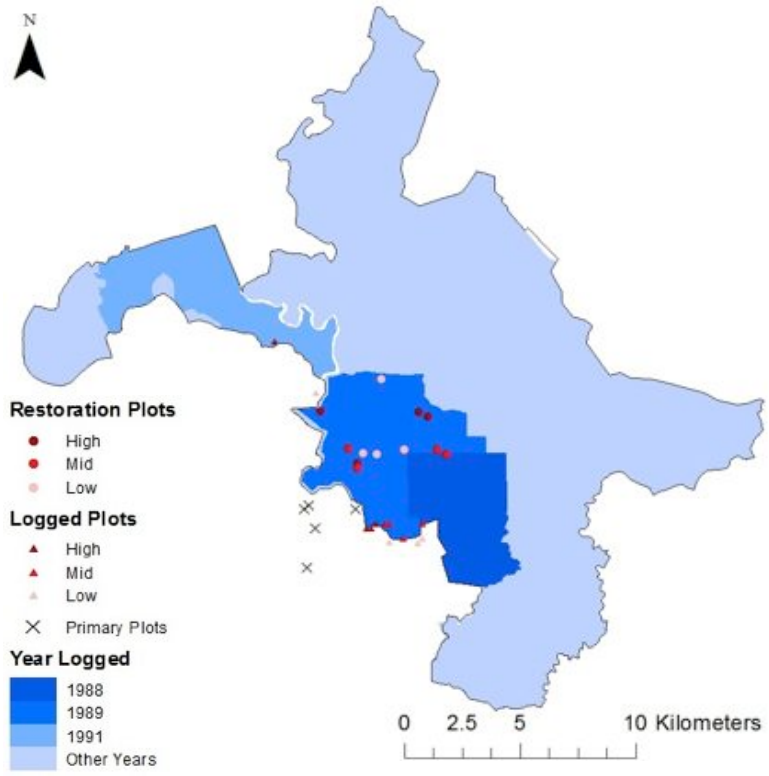

Figure 26. Map showing year of logging in IFAPRO project area, and location of restoration plots (circles), logged plots (triangles), and primary plots (crosses).

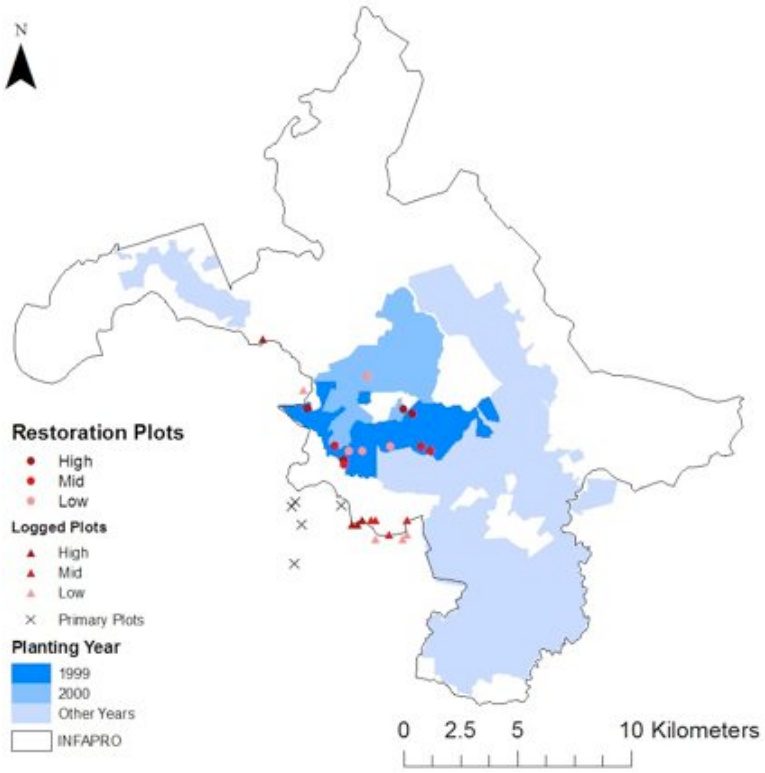

Figure 27. Map showing year of planting in INFAPRO project area, and the location of restoration plots (circles), logged plots (triangles), and primary plots (crosses). White areas are yet to be planted.

Table 21. Criteria for classification of different logging intensities in restoration and logged forest plots.

Logging Intensity category	2015 assessment criteria
Low	No visible skid trails in plot Plot contains ≥1 tree ≥70 cm DBH [a] ≥ 50% of trees (≥30 cm DBH) in circle 1 are Dipterocarps
Mid	Skid trails cover <50% of plot area Plot contains ≥1 tree ≥70 cm DBH [a] Proportion of Dipterocarps intermediate between High and Low category
High	Skid trails cover >50% of plot area Plot contains ≤1 tree ≥70 cm DBH [a] ≤ 50% of trees (≥30 cm DBH) in circle 1 are Dipterocarps

a = A DBH of 70 cm was used as it was assumed that in the approimately 26 years since logging, trees that were just below the 60 cm DBH logging cut off would have had sufficient time for trees to grow >70 cm DBH

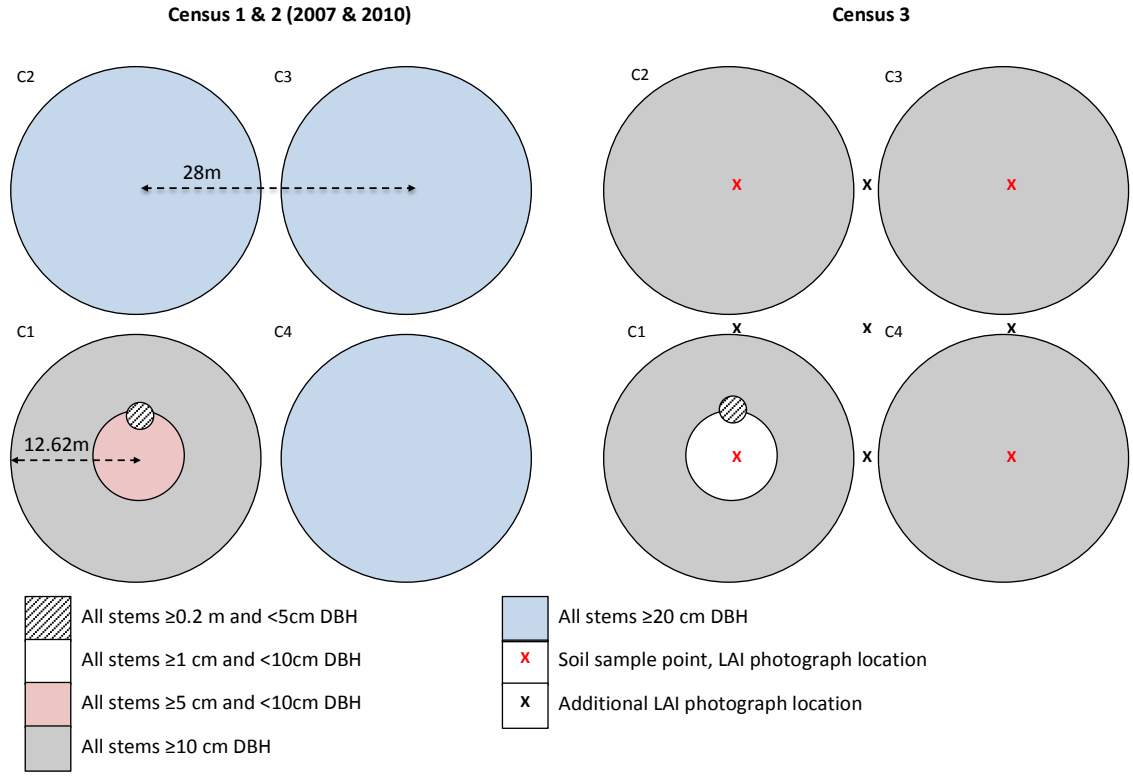

Figure 28. Plot layout in census 1,2 and 3 in restoration and logged forest plots. C1 – 4 refers to circle number.

5.3.3.1.1. Large stems ≥10 cm DBH

In censuses one and two all stems ≥20 cm DBH were measured across the entire plot area (0.2 ha) and in the focal circle (circle one) all stems ≥10 cm DBH were measured (by INFRAPRO, Figure 28). In census three I measured all stems ≥10 cm DBH across the entire plot area (0.2 ha, Figure 28). In primary forest plots all trees ≥10 cm DBH were measured across the entire 1ha plot in all censuses.

For each individual DBH was recorded at 1.3 m, except in the case of trees with buttress roots, diameter was measured 50 cm above the buttress and the point of measurement was recorded. Trees with deformities were measured 2 cm below the deformity in line with standard measurement protocol (See Phillips et al., 2009a). Height was recorded using a handheld Nikon Forestry PRO laser hypsometer. Each individual was identified to

species when possible, if unable to identify an individual to species, samples were collected and stored in order to identify trees to morpho-species.

5.3.3.2.Small stems (1 to 10 cm DBH)

In the centre of circle one a 5 m radius subplot (78.54 m^2) was located (Figure 28). In census one and two all stems between 5 and 10 cm DBH were measured within this subplot (measured by INFAPRO). In census three I measured all stems between 1 and 10 cm DBH within the 5 m radius subplot. For each individual DBH, height and species was recorded.

In two of the five primary forest plots stems between 1 and 10 cm DBH were measured in four subplots of 5 x 15 m (75 m^2, n=8, Figure 29). In the remaining three primary forest plots a 5 m radius circle (78.54 m^2, n=3) was located in the bottom left corner of the plot, with the circle centre at 12.62 m in both *x* and *y* directions (Figure 29).

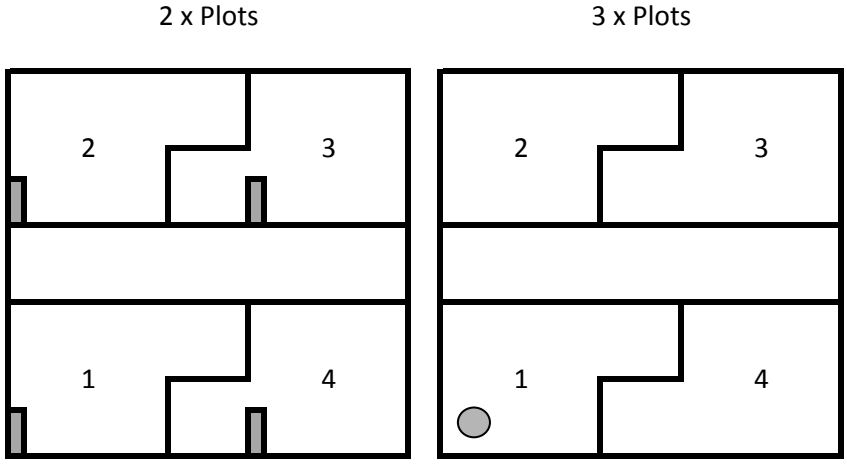

Figure 29. Layout of primary forest plots. Grey areas show where stems 1–10 cm DBH were measured. Numbers 1-4 show position of 0.2 ha subplots used for biodiversity analysis of stems ≥10 cm DBH.

5.3.3.3.Seedling regeneration

In order to assess the regeneration of seedlings a 2 m radius (12.6 m^2) subplot was placed 5 m north of the centre of circle one (Figure 28). If any obstacles such as; streams, large

rocks, large trees with buttress roots or large tree falls covered the subplot area it was rotated 90^0 clockwise. In all censuses all seedling between 0.2 m and 5 cm DBH were recorded. For each individual seedling the height and species was recorded, for any stem <5 cm DBH but >1.3 m height DBH was also recorded.

5.3.3.4.Leaf Area Index

Hemispherical photographs were taken using a 8 mm F3.5 EX DG Fisheye Sigma lens and Canon 350d SLR camera to estimate Leaf area index (LAI). Photographs were taken at the centre of each circle and at 14 m intervals between circle centres to form a grid (n=9, Figure 28). All photos from a single plot were processed together to produce an average LAI value for each plot, using CAN-EYE V6.1 software.

5.3.3.5.Soil sampling

Soil samples were collected in logged (n=3) and restoration (n=3) forest in one of each high, mid, and low intensity plots and in primary foret (n=3). Soil cores, 0-30 cm in depth, were extracted at the centre of each circular subplot (n=4 per plot, Figure 28) using a handheld Edjilcamp soil corer with a 20 mm diameter. Soil cores were divided into four depths; 0-5 cm, 5-10 cm, 10-20 cm and 20-30 cm, air dried and transported for analysis.

Particle size analysis was conducted to determine the proportion of sand, silt and clay in the soil, plus chemical properties carbon and nitrogen percentage, pH, total extractable phosphorus and effective Cation Exchange Capacity (eCEC). Particle size and soil pH were determined following the methods described in Van Reeuwijk (2002), carbon and nitrogen percentage were determined using a gas combustion analyser. Total extractable phosphorus was analysed using a sequential extraction technique as described in Tiessen and Moir (1993). Finally, a modified Silver Thiourea method (Dohrmann, 2006) was used to analyse Cation Exchange Capacity, and eCEC ($mmol^+ kg^{-1}$) was calculated as; Σ Al^{3+}, Ca^{2+}, K^+, Mg^{2+}, Na^+ . For a full explanation of soil analysis see Quesada et al. (2010)

5.3.4. Data standardisation

5.3.4.1.Missing early census diameter measurements of trees 10-20 cm

In census one and two, only trees ≥20 cm DBH were measured in circles 2, 3 and 4 (Figure 28). Therefore the median growth rate was used to estimate the DBH of stems 10-20 cm in circles 2, 3 and 4 in 2007 and 2010. Median growth rate (mm yr^{-1}), was calculated using individuals that were present from census 1 (2007) to census 3 (2015), in circle 1, for the size classes; <10 cm, 10-20 cm, 20-40 cm and >40 cm (Table 2.). Median growth rates were selected as sample sizes are small and typically, growth rate distributions of tropical forests are non-normal. Additionally, a small number of trees >20 cm DBH appear to have been missed in census one or Census two. Therefore, to avoid overestimates of recruitment, the median growth rate for the individuals' size class was used to estimate DBH in the previous census.

Table 22. Median growth rates (mm yr^{-1}) in restoration and logged forest plots.

	Size class	Median growth (mm yr^{-1})	Sample size
Restoration	<10 cm	0.7 (1.4)	31
	10-20 cm	1.9 (0.6)	108
	20-40 cm	3.0 (1.6)	247
	>40 cm	6.7 (1.1)	69
Logged	<10 cm	1.5 (1.6)	27
	10-20 cm	1.8 (1.0)	75
	20-40 cm	4.7 (0.9)	121
	>40 cm	8.3 (1.9)	34

95% confidence intervals are in parentheses.

5.3.4.2.Height diameter allometry

Wood production, mortality losses and AGB stock estimates are improved if tree height is known as well as diameter and species (Chave et al., 2014, Feldpausch et al., 2012). I measured 2025 heights in the plots, which were used to estimate a best-fit height-diameter allometric relationship. This was then used to estimate the heights of trees in the prior censuses. After excluding broken, leaning or severely damaged trees from the analysis, non-linear models were tested. Model fit was compared using Akaike Information Criterion (AIC), and the model with the lowest AIC was selected. The following three-parameter asymptotic model of the form: $y = a - b \exp^{(-cx)}$ had the best model fit (Figure 30a):

$$H = 65.202220066 - 62.36846074 \exp^{(-0.01372362\ D)}$$

Where *H* is height in m and *D* is DBH in cm. This equation was developed using individuals that were between 10 and 149.5 cm DBH and between 5 and 70.2 m in height. For all the individuals that were used to develop the equation, the residual deviation from the model was added to the predicted height at each census interval. This ensured constant growth across all censuses.

The same process was undertaken for the primary forest (179 trees from 10 and 173.8 cm DBH and between 11.2 and 70.2 m) The following three-parameter asymptotic model was found to be the best fit to the data:

$$H = 85.661958625 - 81.041043852 * \exp^{(-0.000860258*D)}$$

Where *H* is height in m and *D* is DBH in mm (Figure 30b).

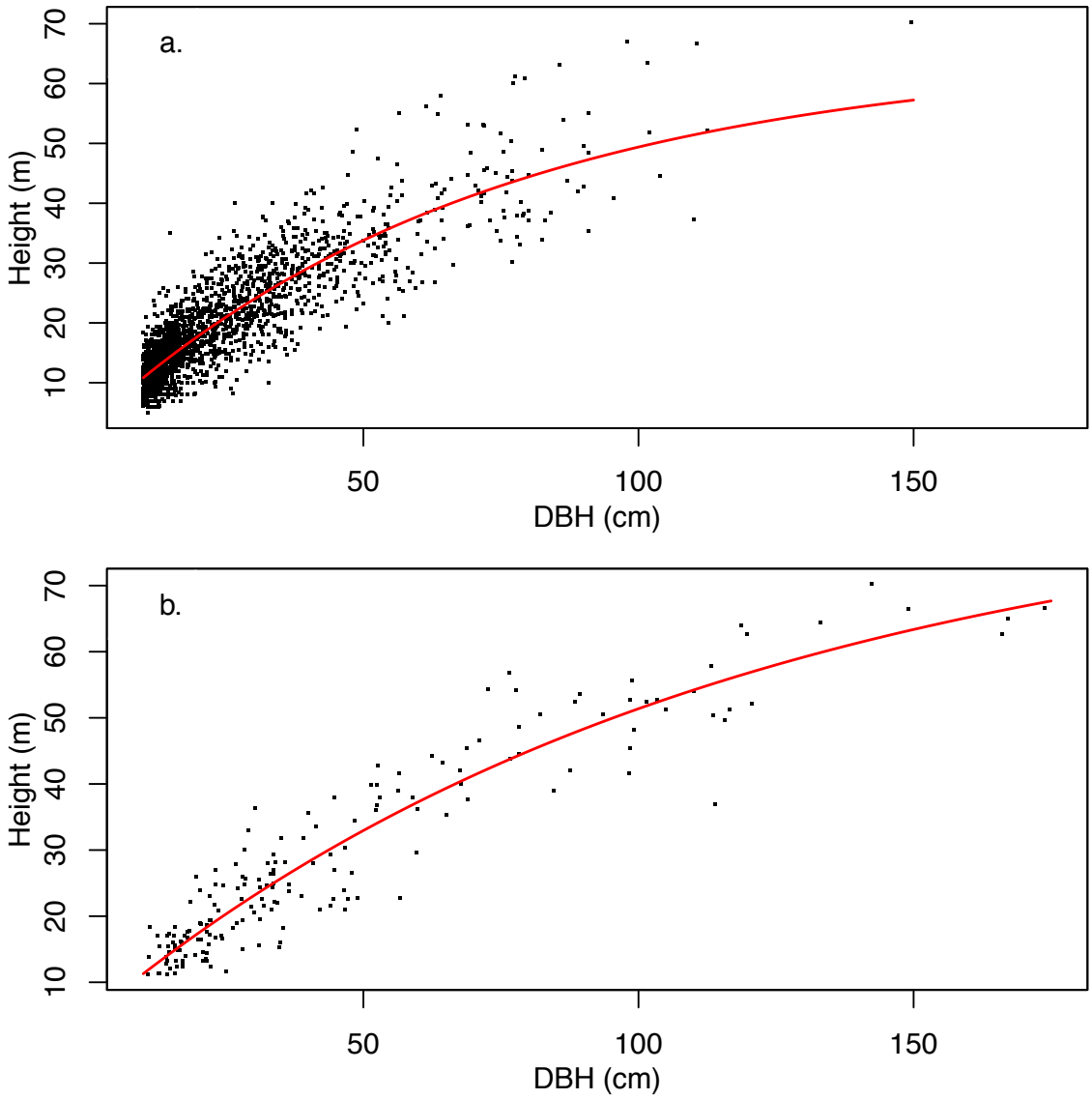

Figure 30. H:DBH allometric relationship for a. logged and restoration plots and b. primary forest plots. Red line shows three-parameter aysmptotic regression line.

5.3.4.3. Point of measurement change and growth anomalies

Any trees that were not measured at 1.3 m (i.e. had a butress or deformity) had the point of measurement (POM) recorded in 2015. For some individuals the POM increased between censuses leading to an apparent drop in DBH, as stems are measured at a higher point on a tapering tree trunk. POM changes were corrected for using the old POM: new POM ratio at the POM change census, this ratio was used to estimate DBH at the old POM and new POM for every census. The mean of these two values was then used in analysis (Talbot et al., 2014).

Each DBH measurement was assessed to see if its growth was unusually small or large. A Tree was considered to be unusually fast growing if DBH had increased by >40 mm yr^{-1} between two consecutive census. These were checked, and if not a continuously fast-growing pioneer species, an individual was assumed to have an error and was correct. Alternatively, if DBH had decreased by >5 mm in total between two census, this was checked and if the tree was not damaged or rotten, this was assumed to be an error. To correct for measurement errors in census 1, DBH was extrapolated backwards from two accurate DBH measurements in census 2 and 3 (n=32). To correct for errors in census 2, DBH was interpolated from the two accurate measurements in census 1 and 3 (n=57). In cases where; there was an error in two censuses or the individual was a new recruit in census 2, the DBH measurement in census 3 was used and the median growth rate for its size class was used to estimate DBH in census 1 and 2 (n=73).

5.3.4.4.Biomass

See section 2.2.1.1 for explanation of AGB calculations. A total of 458 different species were identified (species-specific WD available for 206 species), 65 of which were morpho-species. The genus mean WD was available for 230 species and familial mean WD for 22 species. Aboveground wood production (AGWP), mortality and recruitment were calculated for all three habitats across the whole census interval (2007 to 2015 in logged and restoration plots and 2006 to 2013 in primary forest). AGWP, mortality and recruitment in Mg dry mass ha^{-1} yr^{-1} were calculated as (Talbot et al., 2014):

$$\text{AGWP} = \frac{(\text{Change in AGB of stems from C1 to C3}) + \text{AGB of new stems} \geq 10\text{ cm DBH}}{\text{Census interval}}$$

$$\text{Mortality} = \frac{\text{AGB of stems in C1 that died by C3}}{\text{Census interval}}$$

$$\text{Recruitment} = \frac{\text{AGB of new stems} \geq 10\text{ cm DBH}}{\text{Census interval}}$$

To compare differences in forest structural parameters (AGB, basal area –BA, WD and stem density), AGWP, recruitment, and mortality between logged and restoration forest two-way ANOVA was used. This included a fixed factor of logging intensity to account for differences in high, mid, and low intensity logged plots.

The relative changes in AGB and stem density in logged and restoration forest plots were analysed for each plot at both census intervals (from 2007 to 2010 and from 2010 to 2015), to determine the development stage of each plot following disturbance. Plots were classified as being in one of the three development phases, beginning with a recruitment phase. The recruitment phase was characterised by a high increase in stem density and a relatively small increment of AGB. This was followed by a building phase characterised by larger increments of AGB and an increase stem density. Finally, plots underwent a mature phase, with plots beginning to self-thin, with declining stem density coupled with increases in AGB as large trees become dominant over smaller trees.

5.3.4.5. Biodiversity and species composition ≥10 cm DBH

To compare the tree diversity and species composition between primary, logged and restoration forest, plots of equal size were required. The 1 ha primary forest plots (2006 n=3; 2013 n=5), were each split into four sub-plots, 0.2ha in size, to match the size of logged and restoration plots (Figure 29). This produces a total of 12 primary forest sub-plots in 2006, and 20 primary forest sub-plots in 2013. See section 2.2.1.2 for an explanation of diversity and species composition analysis.

5.3.5. Are differences between logged and restoration forest due to restoration treatment?

Any observed differences in forest recovery between logged and restoration forest could theoretically be a result of one or more of three factors 1) logged and restoration forest differed prior to logging and that difference remains 26 years later, 2) despite carefully matching the characteristics of the logging, the logged and restoration forest were logged differently in terms of volume and/or species extracted, or 3) logged and restoration

forest differed prior to restoration, in terms of forest structure and species composition. Hypotheses one, two, and three were tested and if they were found to be untrue I assumed any observed differences were as a result of the restoration treatment.

H1 - Forest were different prior to logging. Inventory data regarding species composition or forest structure was not collected prior to logging. To determine if logged and restoration forest was different prior to logging, soil physical and chemical properties were compared. This was considered a suitable approach as it has been shown that forest structural properties (AGB, BA, stem density and size distribution) were significantly related to soil properties in Bornean forest (Paoli et al., 2008), as is species composition (Lee et al., 2002).

H2 – Forests allocated to restoration were logged differently. Possible differences in logging between the logged and restoration forest areas were compared using timber extraction data, available on a per compartment basis. All timber extracted was split into seven groups; six from the family *Dipterocarpaceae* and a seventh 'other' group (See Table 23 for a list of species found in each group that were also identified within the study area). Timber extraction data detailed 1) the total volume extracted (m^3 ha^{-1}) from each group and 2) the proportion of all timber extracted per group. Logged and restoration forest was compared using t-tests, p values were adjusted using the Benjamini-Hochberg correction to correct for any type 1 errors.

Table 23. Details of timber groups showing genus and species within groups.

Group name	Genus	Species
White seraya	*Parashorea*	*P. tomentella, P. malaanonan*
Red seraya	*Shorea*	*S. argentifolia, S. ovalis, S. parvifolia, S. beccariana, S. fallax, S. johorensis, S. leprosula, S. macroptera*
Yellow seraya	*Shorea*	*S. gibbosa, S. xanthophylla, S. acuminatissima, S. faguetiana*
Kapur	*Dryobalanops*	*D.lanceolata*
Keruing	*Dipterocarpus*	*D. kerrii, D. applanatus, D. caudiferus, D. conformis, D. gracilis, D. lowii*
Selangan batu	*Shorea*	*S. atrinervosa, S. falciferoides, S. guiso, S. seminis, S. superba*
Other	Other Spp.	No information of specific species available

Only species that were observed in census 3 are shown.

H3 – Forest were different prior to restoration. Theoretically, if logged and restoration forest areas were the same prior to logging (*H1* null) and were logged the same (*H2* null), they would be recovering at the same rate and forest structure should be the same prior to restoration. Then, at the time of restoration, recovery would diverge, between areas that were restored and areas that were left to naturally regenerate. However, it is possible the forest were different prior to restoration. No inventory data was collected prior to restoration work (in 1999/2000), therefore data from census 1 (2007) was used instead as it is most similar to initial site conditions. Analysis of covariance (ANCOVA) was used to compare AGB accumulation (Mg ha^{-1} yr^{-1}) with forest structural parameters (AGB, BA, WD, and stem density) in 2007, between logged and restoration forest. This allowed me to compare AGB accumulation in logged and restoration forest, whilst controlling for differences in forest structure

Principal components analysis was used to reduce multiple variables related to forest structure and composition (AGB, BA, WD and stem density) into 2 principal component axes. Principal component axis 1 (PC1) explained 66.5% of the variation and was related to AGB, BA and stem density, whilst PC2 explained 25% of the variation and was related to wood density, which in turn is determined by species composition. Therefore PC1 was related to forest structure and PC2 was related to species composition. I then undertook

two ANCOVA analysis, comparing AGB accumulation in logged and restoration forest, using PC1 and PC2 as covariates, respectively. This allowed me to compare differences in AGB accumulation whilst accounting for differences in forest structure and species composition.

5.4. Results

5.4.1. Forest structure and biodiversity

5.4.1.1.AGB and forest structure of trees ≥5 cm DBH

5.4.1.1.1. AGB

Aboveground biomass increased over time in logged and restoration forest plots, with restoration and primary forest having significantly more AGB than logged forest by 2015 ($F = 6.7$, $df = 2$, $p = 0.004$, Figure 31a). Over eight years, between census 1 and census 3, the rate of AGB accumulation in restoration plots was significantly higher than in logged forest plots, at 7.8 Mg ha^{-1} yr^{-1} and 3.5 Mg ha^{-1} yr^{-1}, respectively ($F = 9.6$, $df = 1$, $p = 0.006$, Table 24).

Total AGB was correlated with estimated logging intensity: low intensity plots had significantly higher AGB than high intensity plots, with on average, three times greater AGB in logged forest, and two times greater AGB in restoration forest in 2015 (Table 25). In logged and restoration plots an additional 7.1 Mg ha^{-1} and 11.6 Mg ha^{-1} respectively was found in small stems (5-10 cm DBH). However, AGB of small stems did not differ significantly ($F = 2.6$, $df = 1$, $p = 0.1$) between habitats or logging intensities (Table 25).

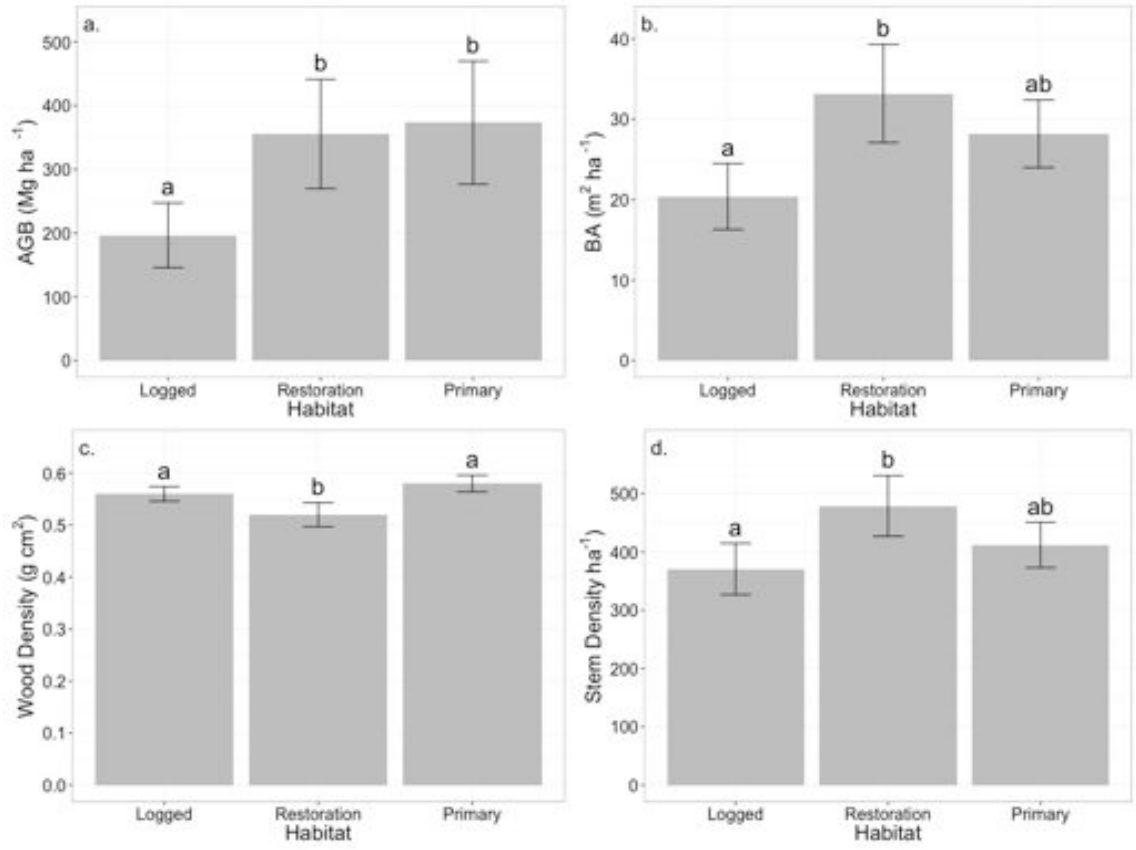

Figure 31. Mean a. AGB (Mg ha^{-1}), b. BA (m^3 ha^{-1}), c. wood density (g cm^3), and d. stems density (ha^{-1}) for stems ≥10 cm DBH, in logged, restoration and primary forest, in 2015 Error bars show 95% CI, letters show significant differences from one-way ANOVA.

Table 24. Mean slope from linear regression of time (2007 - 2015) against AGB, BA, Stems and WD in logged and restoration forest plots at high, mid and low logging intensity, with overall mean for all logged and all restoration forest plots

		AGB (Mg ha^{-1} yr^{-1})	BA (m^3 ha^{-1} yr^{-1})	Stems (ha^{-1} yr^{-1})	WD (g cm^3 yr^{-1})
Logged	High	2.5 (1.0)[a]	0.4 (0.1)[a]	13.2 (6.6)[a]	0.001 (0.002)
	Mid	3.3 (4.4)[a]	0.1 (0.5)[a]	1.9 (5.8)[a]	0.002 (0.004)
	Low	4.6 (3.0)[a]	0.4 (0.3)[a]	1.8 (3.1)[a]	0.001 (0.001)
	Mean	3.5 (1.7)[a]	0.3 (0.2)[a]	4.7 (4.0)[a]	0.002 (0.001)[a]
Restoration	High	5.0 (2.4)[a]	0.5 (0.3)[a]	10.8 (4.5)[a]	0.003 (0.002)
	Mid	7.3 (5.3)[a]	0.4 (0.4)[a]	4.1 (4.5)[ab]	0.002 (0.002)
	Low	11.1 (2.0)[a]	0.6 (0.2)[a]	-0.8 (3.5)[b]	0.001 (0.001)
	Mean	7.8 (2.4)[b]	0.5 (0.2)[b]	5.6 (4.2)[a]	0.001 (0.001)[a]

95% CI shown in parentheses. Letters denote significant differences between logged and restoration forest mean values.

5.4.1.1.2. Basal area, wood density and stem density

Changes in AGB may be explained by changes in basal area, wood density and stem density, which are considered in turn. On average BA increased over time and by 2015, BA in restoration forest was indistinguishable from the level in primary forest (Table 25, Figure 31b), and significantly higher than logged forest ($F = 6.8$, $df = 2$, $p = 0.004$, Figure 31b). The rate of BA accumulation was marginally greater in restoration forest than logged forest ($F = 3.6$, $df = 1$, $p = 0.07$, Table 24). As with AGB, total BA increased as logging intensity decreased; restoration forest plots had significantly greater BA in low intensity plots compared to high intensity plots ($p = <0.001$), however, these differences were not significant in logged forest (Table 25). Restoration forest had significantly higher BA in small stems ($F = 4.4$, $df = 2$, $p = 0.05$), than logged forest, but there was no difference due to logging intensity (Table 25).

Wood density (WD) increased slightly overtime in both logged and restoration forest plots (Table 25). By 2015, restoration forest had significantly lower WD than both logged and primary forest ($F = 8.7$, $df = 2$, $p = 0.001$, Figure 31c). However, WD did not differ in relation to logging intensity (Table 24, Table 25).

Mean stem density also increased over time in both logged and restoration forest plots (Table 25), and by 2015, restoration forest had significantly more stems than logged forest ($F = 5.6$, $df = 2$, $p = 0.009$, Figure 31d). However, despite difference in stem density the recruitment of new stems (≥10cm DBH) was indistinguishable between logged and restoration forest (Table 24). Stem density increased as logging intensity decreased, but not significantly so (Table 25). Despite high intensity plots having lower stem density they also had the highest recruitment of new stems (Table 24), with high intensity restoration plots recruiting marginally more new stems than low intensity plots ($p = 0.07$). By 2015 restoration forest had 775 small stems ha^{-1}, higher than the 479 stems ha^{-1} in logged forest, but not significantly so (Table 25).

In 2015 the frequency distribution of stems in both logged and restoration forest resembled the inverse J shape typical of primary forest; with no significant differences in stem density in any size class, except stems 1-2 cm 32-64cm ($F = 2.9$, $df = 6$, $p = <0.001$, $p_{adj} = 0.003$ – Bonferroni corrected p value; Figure 32). Furthermore, despite logged and

restoration forest having high biomass they still lack the very large trees (≥128 cm) that are present in primary forest (n=5 trees ≥128 cm in primary forest).

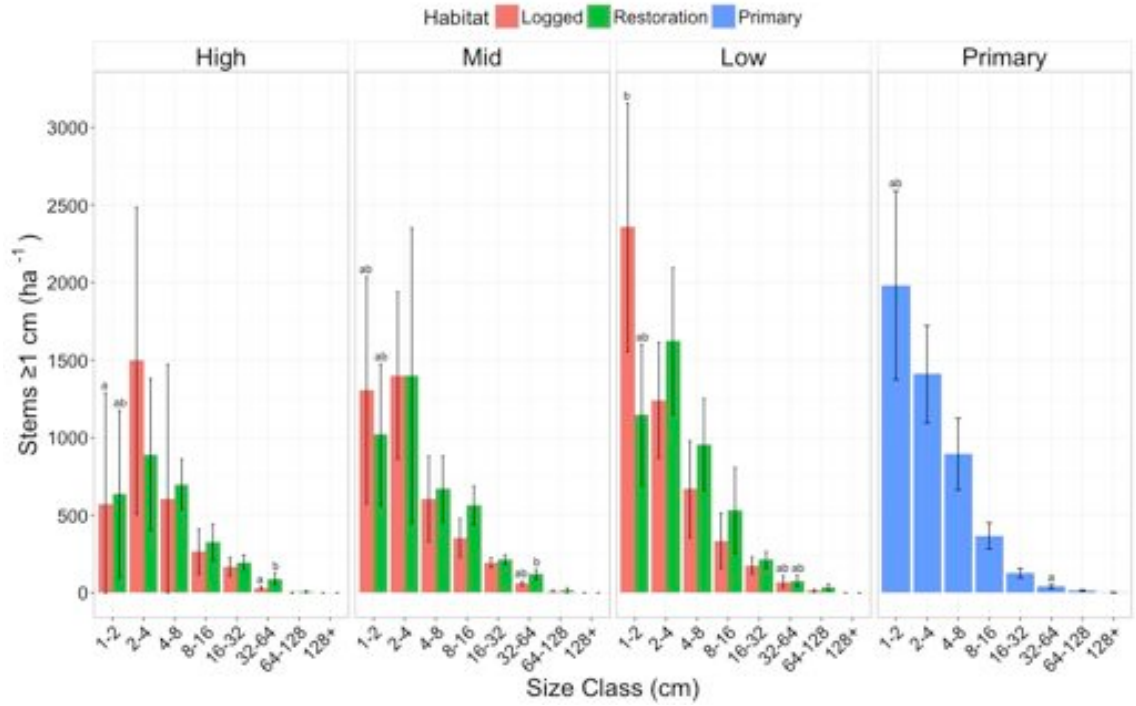

Figure 32. Freqency distribution of stems ≥1 cm DBH in logged, restoration and primary forest in 2015. Error bars show 95% CI. Letters show significant differences in stem density between logged, restoration and primary forest within a size class, only shown in size classes where significant differences are present.

5.4.1.2.AGB and forest structure of trees ≤5 cm DBH

In comparison to primary forest the AGB of stems between 1 and 5 cm DBH was significantly lower in restoration forest ($p = 0.02$) and marginally lower in logged forest, but not significantly so ($p = 0.07$, Table 25). Meanwhile, BA was the same among habitats (Table 25). The observed differences in AGB were due to significantly fewer stems in restoration forest compared to primary forest ($p = 0.03$), and significantly lower wood density in both logged ($p = 0.03$) and restoration ($p = 0.009$) forest compared to primary forest (Table 25).

		AGB (Mg ha^{-1})				BA (m^3 ha^{-1})			
		Large stems (≥10 cm DBH)							
		High (n=4)	Mid (n=4)	Low (n=4)	Mean (n=12)	High (n=4)	Mid (n=4)	Low (n=4)	Mean (n=12)
Logged	2007 (n=12)	62.5 (11.1)	216.8 (31.4)	221.7 (18.9)	167.0 (45.2)	8.5 (1.8)	22.3 (3.4)	22.7 (2.6)	17.9 (4.2)
	2010 (n=12)	78.0 (14.3)	243.0 (33.9)	250.5 (25.0)	190.5 (48.9)	10.9 (1.8)	24.4 (3.2)	25.1 (3.7)	20.1 (4.2)
	2015 (n=12)	83.5 (16.0)^{a}	245.8 (52.3)^{ab}	260.6 (23.8)^{b}	196.6 (50.7)^{a}	11.7 (1.9)^{a}	23.6 (3.4)^{a}	25.8 (4.3)^{a}	20.4 (4.1)^{a}
Restoration	2007 (n=12)	183.7 (78.0)	278.1 (70.7)	412.8 (137.3)	291.5 (76.2)	21.6 (9.7)	27.7 (7.1)	36.8 (10.2)	28.7 (6.0)
	2010 (n=12)	213.7 (95.8)	305.9 (64.8)	459.3 (141.7)	326.3 (81.4)	25.4 (10.9)	30.1 (7.7)	40.1 (10.4)	31.9 (6.3)
	2015 (n=12)	225.8 (95.7)^{a}	337.1 (68.5)^{ab}	503.5 (130.4)^{b}	355.5 (85.7)^{b}	26.1 (10.4)^{a}	31.3 (7.1)^{ab}	42.2 (9.1)^{b}	33.2 (6.1)^{b}
Primary	2006 (n=3)				333.7 (89.3)				27.3 (3.3)
	2013 (n=5)				373.2 (96.5)				28.2 (4.2)
		Small stems (5 - 10 cm DBH)							
Logged	2007 (n=12)	3.8 (2.9)	6.0 (1.7)	7.0 (4.9)	5.6 (2.0)	1.1 (0.9)	1.8 (0.5)	1.8 (1.3)	1.6 (0.5)
	2010 (n=12)	5.6 (3.9)	8.5 (2.9)	8.3 (5.9)	7.4 (2.4)	1.6 (1.3)	2.5 (0.8)	2.1 (1.6)	2.1 (0.7)
	2015 (n=12)	3.7 (4.2)^{a}	6.8 (2.8)^{a}	10.3 (8.8)^{a}	7.1 (4.0)^{a}	1.4 (1.5)^{a}	2.1 (0.6)^{a}	2.5 (1.9)^{a}	2.0 (0.9)^{a}
Restoration	2007 (n=12)	4.0 (2.4)	6.5 (2.8)	14.6 (12.5)	8.4 (4.7)	1.1 (0.7)	2.1 (0.9)	3.9 (3.3)	2.4 (1.2)
	2010 (n=12)	5.9 (3.7)	10.5 (3.9)	19.1 (15.1)	11.8 (5.8)	1.6 (1.1)	3.2 (1.1)	5.0 (3.7)	3.3 (1.5)
	2015 (n=12)	6.8 (2.6)^{a}	12.6 (5.9)^{a}	15.5 (9.5)^{a}	11.6 (4.1)^{a}	2.3 (0.9)^{a}	3.9 (1.2)^{a}	4.2 (2.3)^{a}	3.5 (1.0)^{b}
Primary	2015 (n=11)				9.9 (2.0)				2.5 (0.4)
		Stems 1 – 5 cm DBH							
Logged	2015 (n=12)	3.2 (3.3)^{a}	3.1 (1.0)^{a}	3.4 (1.1)^{a}	3.2 (1.1)^{a}	1.6 (1.3)^{a}	1.6 (0.5)^{a}	1.6 (0.3)^{a}	1.6 (0.4)^{a}
Restoration	2015 (n=12)	2.0 (0.7)^{a}	2.9 (2.6)^{a}	3.9 (1.3)^{a}	2.9 (1.0)^{a}	1.1 (0.4)^{a}	1.4 (1.0)^{a}	1.7 (0.6)^{a}	1.4 (0.4)^{a}
Primary	2015 (n=12)				4.9 (0.7)^{b}				1.8 (0.3)^{a}

Table 25. AGB (Mg ha^{-1}), BA (m^3 ha^{-1}), wood density (g cm^3) and stems density (ha^{-1}) for stems ≥10 cm DBH, 5-10 cm DBH and 1-10 cm DBH in logged, restoration and primary forest plots at each census. Logged and restoration forest plots are split into high, medium and low intensity logging plots, with overall mean shown. 95% confidence intervals in parentheses.

		Stem Density (ha^{-1})				Wood Density ($g\ cm^3$)			
		High (n=4)	Mid (n=4)	Low (n=4)	Mean (n=12)	High (n=4)	Mid (n=4)	Low (n=4)	Mean (n=12)
Logged	2007 (n=12)	204 (29)	375 (33)	389 (106)	323 (61)	0.54 (0.04)	0.54 (0.04)	0.57 (0.01)	0.55 (0.02)
	2010 (n=12)	289 (41)	398 (16)	404 (108)	363 (47)	0.55 (0.04)	0.55 (0.03)	0.57 (0.00)	0.56 (0.02)
	2015 (n=12)	316 (68)[a]	393 (32)[a]	405 (97)[a]	371 (44)[a]	0.55 (0.04)[a]	0.56 (0.02)[a]	0.57 (0.00)[a]	0.56 (0.01)[a]
Restoration	2007 (n=12)	353 (149)	463 (108)	495 (93)	437 (71)	0.47 (0.03)	0.51 (0.06)	0.53 (0.04)	0.50 (0.03)
	2010 (n=12)	431 (137)	498 (105)	510 (90)	480 (62)	0.48 (0.02)	0.51 (0.06)	0.53 (0.04)	0.51 (0.03)
	2015 (n=12)	446 (108)[a]	499 (97)[a]	491 (79)[a]	479 (52)[b]	0.50 (0.03)[a]	0.52 (0.06)[a]	0.54 (0.03)[a]	0.52 (0.02)[b]
Primary	2006 (n=3)				424 (54)				0.58 (0.02)
	2013 (n=5)				412 (39)				0.58 (0.02)
					5 - 10 cm DBH				
Logged	2007 (n=12)	286 (213)	446 (125)	414 (295)	382 (123)	0.63 (0.1)	0.57 (0.1)	0.60 (0.1)	0.60 (0.0)
	2010 (n=12)	286 (213)	605 (157)	446 (330)	446 (149)	0.63 (0.1)	0.56 (0.1)	0.60 (0.1)	0.59 (0.1)
	2015 (n=12)	382 (400)[a]	477 (125)[a]	605 (450)[a]	479 (223)[a]	0.50 (0.1)[a]	0.57 (0.0)[a]	0.58 (0.1)[a]	0.55 (0.0)[a]
Restoration	2007 (n=12)	286 (187)	509 (176)	859 (597)	552 (241)	0.58 (0.1)	0.50 (0.1)	0.56 (0.1)	0.55 (0.0)
	2010 (n=12)	382 (306)	700 (161)	1050 (663)	711 (277)	0.62 (0.1)	0.51 (0.1)	0.57 (0.1)	0.57 (0.1)
	2015 (n=12)	573 (239)[a]	828 (239)[a]	923 (471)[a]	775 (198)[a]	0.58 (0.1)[a]	0.50 (0.1)[a]	0.56 (0.1)[a]	0.55 (0.0)[a]
Primary	2015 (n=11)				656 (115)				0.60 (0.0)
					1 - 5 cm DBH				
Logged	2015 (n=12)	2483 (1807)[a]	3088 (639)[a]	3979 (1056)[a]	3183 (753)[ab]	0.49 (0.0)[a]	0.56 (0.0)[a]	0.58 (0.1)[a]	0.55 (0.0)[a]
Restoration	2015 (n=12)	1878 (974)[a]	2642 (1653)[a]	3215 (1080)[a]	2578 (739)[a]	0.54 (0.0)[a]	0.52 (0.1)[a]	0.56 (0.0)[a]	0.54 (0.0)[a]
Primary	2015 (n=12)				3939 (568)[b]				0.56 (0.0)

Table 22 continued.

5.4.1.3.Above ground wood production, Recruitment and Mortality of stems ≥10 cm DBH

Mean AGWP is marginally different among habitats (F = 3.0, df = 2, p = 0.07). AGWP in restoration forest was indistinguishable from primary forest, whereas logged forest was marginally lower compared to restoration forest (p = 0.07, Figure 33). In both logged and restoration forest plots, AGWP increased as the intensity of logging decreased, with high intensity restoration plots having a significantly higher rate of AGWP (p = 0.001) than low intensity plots (Table 26).

AGWP is composed of wood production in surviving stems and production from newly recruited stems. The mean AGWP of recruits in primary forest was twice that of logged (p = 0.07) and restoration forest (p = 0.01, Figure 33). However, there was no effect of logging intensity on recruitment (Table 26).

Whilst primary forest had the highest AGWP of recruits, it also had the lowest AGB mortality losses, significantly lower than observed in logged forest plots (p = 0.05, Figure 33). Mortality in restoration plots was also higher than primary forest but not significantly so. There was no trend in AGB mortality losses with logging intensity (Table 26).

Table 26. AGWP, recruitment and mortality (Mg ha^{-1} yr^{-1}), for high, mid and low intensity plots in restoration, logged and primary forest

		AGWP	Recruitment	Mortality
Restoration	High	8.0 (2.7)[a]	0.3 (0.1)[a]	2.4 (1.8)[a]
	Mid	9.6 (4.6)[ab]	0.2 (0.1)[a]	2.5 (1.3)[a]
	Low	14.4 (1.9)[b]	0.2 (0.1)[a]	2.0 (2.2)[a]
Logged	High	3.8 (0.8)[a]	0.3 (0.1)[a]	1.7 (0.9)[a]
	Mid	8.5 (2.0)[a]	0.3 (0.1)[a]	4.2 (2.1)[a]
	Low	9.7 (3.0)[a]	0.2 (0.2)[a]	4.0 (1.0)[a]

95% CI in parentheses. Letters denote significant differences.

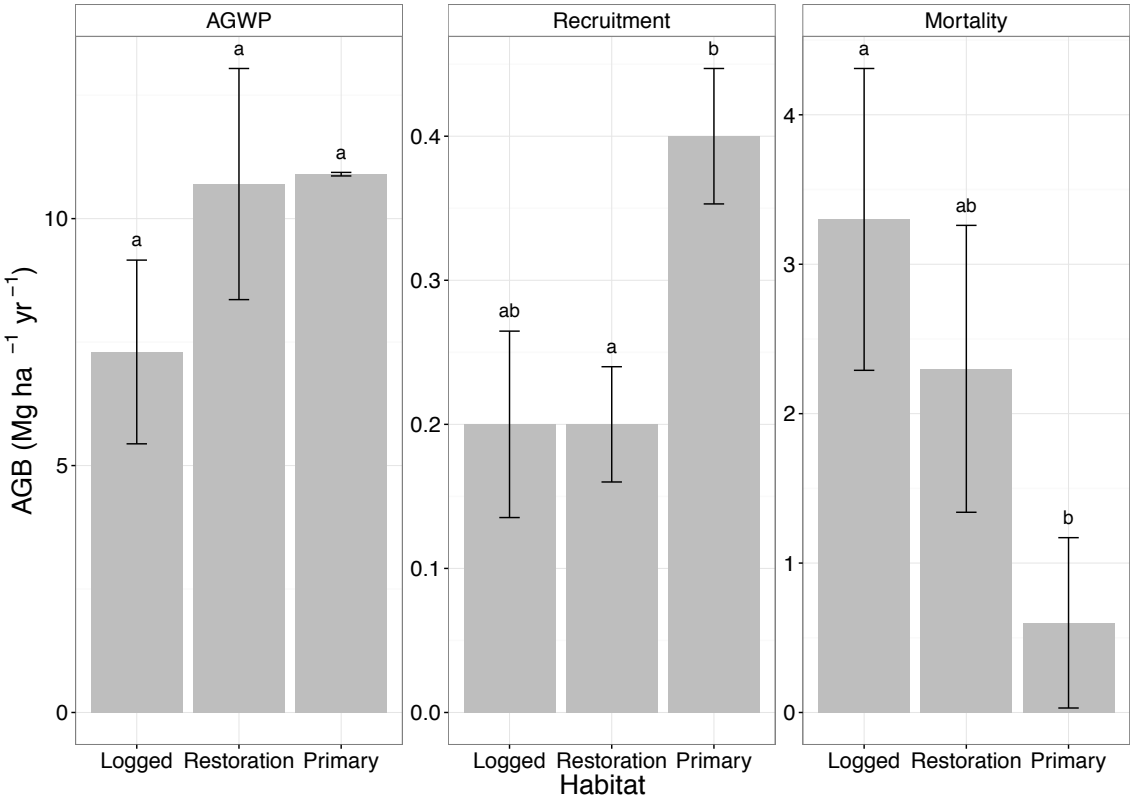

Figure 33. AGWP, recruitment and mortality (Mg ha^{-1} yr^{-1}) in restoration, logged forest and primary forest. Error bars show 95% CI. Letters denote significant differences.

5.4.1.4.Development phase

On average low intensity plot in both restoration and logged forest were in a recruitment phase. Albeit, with logged forest having lower AGB and stem density (Figure 34a and b). In restoration forest, mid and low intensity plots were in a building phase between census one and two (Figure 34a). Mid and low intensity plots in logged forest were also in a recovery phase over the entire census period (2007 to 2015, Figure 34b). Between censuses two and three, restoration plots were in a mature phase, beginning to reduce in stem density but increasing in AGB. Primary forest plots were also in a mature phase (Figure 34a).

Generally, the differences in development between mid and low intensity logged forest plots were much smaller than those observed in mid and low intensity restoration forest plots. The differences between logged and restoration forest suggests that logged forest plots were at an earlier stage of development; still undergoing growth and recruitment to reach primary forest AGB and stem density. Whereas restoration plots in some cases had attained or were approaching primary forest AGB and were undergoing self-thinning, suggesting they were at a later stage of development.

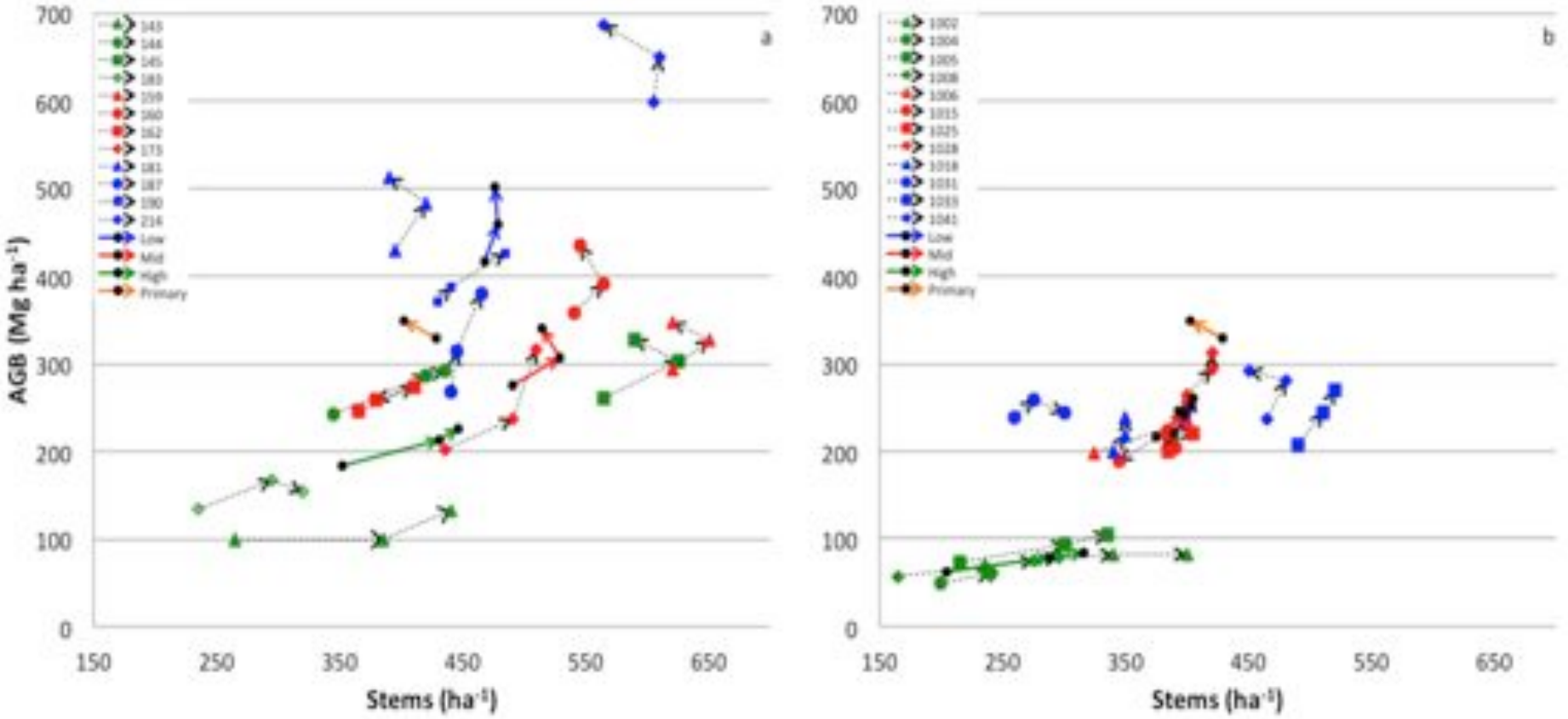

Figure 34. Temporal changes in stem density (≥10 cm DBH ha^{-1}) and AGB (Mg ha^{-1}) between census 1 and 3, in a) restoration forest and b) logged forest. Dotted lines and arrows show change between census 1 to 2 and census 2 to 3 for each plot. Thick coloured lines and arrows shows the mean changes for high, mid and low intensity logging plots and for primary forest.

5.4.1.5.AGB of planted stems

Planting lines were identified in every restoration plot, with an average of four planting lines per plot, and signs of liberation cutting (i.e. the tending of naturally regenerating seedlings to remove climbers) found in seven of the 12 plots, in 2015, 12 years after liberation cutting ended. In the restoration plots, just 18 planted stems were found, located in five plots (two medium and three high intensity plots). These planted individuals were dipterocarps, of six different species, (mean DBH of 5.9 cm, range 1-17.9 cm; mean height 7.5 m, range 1.2-19.6 m; mean AGB, per plot (0.2 ha) 88.5 kg (range 0.03-322 kg). Thus enrichment planting itself may not be the most important restoration treatment intervention.

5.4.1.6.Leaf area index

LAI, is identical in logged and primary forest (Table 27), whilst restoration forest has significantly lower LAI than logged forest ($p = 0.05$). However, percentage canopy cover is indistinguishable among logged, restoration and primary forest (Table 27). Logging intensity had no effect on either LAI ($F = 2.6$, $df = 2$, $p = 0.1$) or canopy cover ($F = 2.1$, $df = 2$, $p = 0.2$).

Table 27. Leaf are index and percentge caonpy cover in Logged, restoration and primary forest in 2015

		LAI	% Cover
Restoration	High	5.5 (0.4)	83 (3)
	Mid	5.0 (0.5)	86 (6)
	Low	4.7 (0.4)	87 (6)
	Mean	5.1 (0.3)[a]	85 (3)[a]
Logged	High	5.6 (0.5)	83 (6)
	Mid	5.8 (0.6)	88 (6)
	Low	5.3 (0.5)	88 (3)
	Mean	5.6 (0.3)[b]	87 (3)[a]
Primary		5.6 (0.5)[ab]	83 (3)[a]

. 95% CI in parentheses. Letters denote significant difference.

5.4.1.7.Biodiversity and species composition

5.4.1.7.1. α and β diversity of trees >10 cm DBH

The α-diversity of trees ≥10 cm DBH increases over time. By 2015, restoration forest plots had species richness (N_0) indistinguishable to primary forest plots. However, logged forest had significantly fewer species per plot than restoration forest (p = <0.001) and primary forest (p = <0.001). Species evenness (N_2) in logged forest was also significantly lower than seen in restoration forest (p = 0.009) and primary forest (p = <0.001), which could suggest a dominance of a small number of species common in logged forest (Table 29).

As logging intensity decreased both species richness and evenness increased in restoration and logged forest (Table 29). High intensity plots in logged forest had significantly lower species richness and evenness than both mid and low intensity plots. However, in restoration forest there was no significant effect of logging intensity on spices richness or evenness (Table 29).

Sørensen similarity scores (a measure of β-diversity) was very low, with β diversity scores of <0.16 in all cases (Table 28), which suggests that the species composition amongst logged, restoration and primary forest areas differs.

Table 28. Sørensen similarity scores for logged, resotration and primary forestα diversity of trees <10 cm DBH

		Restoration			Primary	
		2007	2010	2015	2006	2013
Logged	2007	0.15			0.10	
	2010		0.16			0.11
	2015			0.16		0.11
Restoration	2007				0.13	
	2010					0.14
	2015					0.15

5.4.1.7.2. α and β diversity of trees <10 cm DBH

Mean species richness and evenness in stems 5 - 10 cm DBH increases between 2007 and 2015 in both logged and restoration forest (Table 29). By 2015 logged forest had significantly fewer species than restoration forest (p = <0.001) and primary forest (p =

<0.001). Species evenness was also significantly lower in logged forest, than restoration (p = 0.05) and primary forest (p = 0.009, Table 29).

However, when considering all stems 1-10 cm DBH, both logged and restoration forest had significantly fewer species than primary forest (logged; p = <0.001, restoration; p = 0.005). Species evenness of stems 1-10 cm DBH was also significantly lower than primary forest (p = 0.01, Table 29).

As was the case for large stems ≥10 cm DBH, an increase in logging intensity corresponded with a decrease in species richness and evenness for both 1-10 cm and 5-10 cm DBH size classes. However, the effect of logging intensity on species richness and evenness was not significant between different logging intensities (Table 29).

		N_0 = Species Richness				N_2 = Inv Simpsons *D*			
		≥10 cm DBH							
		High	Mid	Low	Mean	High	Mid	Low	Mean
Logged	2007	13.5 (5.3)	38.5 (5.0)	42.8 (8.8)	31.6 (8.4)	1.8 (0.7)	3.3 (0.4)	3.5 (0.2)	2.9 (0.5)
	2010	19.3 (8.4)	40.0 (4.7)	43.8 (10.0)	34.3 (7.6)	2.2 (0.9)	3.4 (0.3)	3.5 (0.2)	3.0 (0.5)
	2015	20.0 (8.5)[a]	40.8 (4.6)[b]	43.0 (10.1)[b]	34.6 (7.4)[a]	2.2 (0.8)[a]	3.4 (0.2)[b]	3.5 (0.2)[b]	3.1 (0.4)[a]
Restoration	2007	31.3 (2.7)	43.0 (6.4)	54.0 (1.4)	42.8 (5.9)	2.9 (0.4)	3.2 (0.5)	3.7 (0.2)	3.3 (0.3)
	2010	38.3 (3.3)	47.0 (7.3)	55.3 (2.0)	46.8 (4.8)	3.1 (0.5)	3.4 (0.5)	3.7 (0.1)	3.4 (0.2)
	2015	40.3 (5.8)[a]	50.3 (6.2)[a]	53.0 (2.4)[a]	47.8 (4.2)[b]	3.2 (0.5)[a]	3.5 (0.4)[a]	3.7 (0.1)[a]	3.5 (0.2)[b]
Primary	2006				46.0 (3.7)				3.6 (0.1)
	2013				46.0 (2.9)[b]				3.6 (0.1)[b]
		5 - 10 cm DBH							
Logged	2007	2.0 (1.6)	3.0 (0.8)	3.0 (2.4)	2.7 (0.9)	2.0 (1.6)	2.8 (0.8)	3.0 (2.4)	2.6 (0.9)
	2010	1.5 (1.0)	4.0 (0.8)	2.8 (2.2)	2.8 (1.0)	1.5 (1.0)	3.9 (0.8)	2.6 (2.0)	2.7 (0.9)
	2015	2.0 (2.1)[a]	3.8 (1.2)[a]	3.3 (2.2)[a]	3.0 (1.1)[a]	1.7 (1.7)[a]	3.8 (1.2)[a]	2.8 (1.7)[a]	2.8 (0.9)[a]
Restoration	2007	2.0 (1.8)	2.8 (0.9)	5.5 (3.3)	3.4 (1.5)	2.0 (1.8)	2.5 (0.9)	4.8 (2.4)	3.1 (1.2)
	2010	2.5 (2.3)	3.8 (0.9)	6.8 (3.3)	4.3 (1.6)	2.4 (2.2)	3.4 (1.0)	5.7 (2.0)	3.8 (1.2)
	2015	3.8 (1.7)[a]	4.8 (0.9)[a]	6.0 (2.1)[a]	4.8 (1.0)[b]	3.4 (1.5)[a]	4.3 (1.0)[a]	5.2 (1.5)[a]	4.3 (0.8)[b]
Primary	2015				5.6 (1.3)[b]				5.4 (1.4)[b]
		1 - 10 cm DBH							
Logged	2015	6.5 (5.0)[a]	14.3 (3.2)[a]	15.3 (8.1)[a]	12.0 (3.8)[a]	3.9 (3.1)[a]	9.4 (4.2)[a]	7.8 (4.8)[a]	7.0 (2.5)[a]
Restoration	2015	10.8 (4.7)[a]	15.8 (6.3)[a]	16.3 (3.3)[a]	14.3 (3.0)[a]	7.4 (3.0)[a]	11.0 (4.1)[a]	9.8 (5.2)[a]	9.4 (2.4)[ab]
Primary	2015				21.9 (2.8)[b]				13.5 (3.3)[b]

Table 29. Hill numbers N_0 and N_2 for logged, restoration and primary forest plots at high, mid and low logging intensities at all time periods, for stems ≥10 cm DBH, 5-10 cm DBH and 1-10 cm DBH. 95% CI in parentheses. Letters denote significant differences.

5.4.1.7.3. Species composition of stems ≥ 10 cm DBH

Non-metric multidimensional scaling shows that there is still a markedly different species composition in primary forest plots compared to both logged and restoration forest plots at each census. With primary forest points clustered in the top right of the plot, and logged and restoration points clustered towards the centre plot (Figure 35). There were similarities in the species composition of logged and restoration plots, with points being overlaid (Figure 35).

Notably, high intensity logged forest plots were all grouped to the top left, the very different composition of these plots could be due to the high intensity of logging or could indicate that these plots had a different species composition prior to logging. These high intensity logged forest plots were located close to the genera; *Endospermum, Pterospermum, Duabanga* and *Octomeles* (Figure 35), which were all fast growth species (Saner et al., 2012) common in logged forest and were indicative of high levels of disturbance. Many of the genera within the Dipterocarpaceae family were overlaid with logged and restoration plots (Figure 35), showing that these genera were common within the logged and restoration forest despite being preferentially targeted during logging activities.

When mean NMDS scores in logged and restoration forest for census one (2007) and census three (2015) were plotted, a shift in species composition in the direction of primary forest plots is observed (Figure 36). This suggests that in the eight years between censuses one and three the species composition of plots is becoming more similar to primary forest, however, species composition is still markedly different and therefore it may take some time before restoration and logged forest is similar to primary forest.

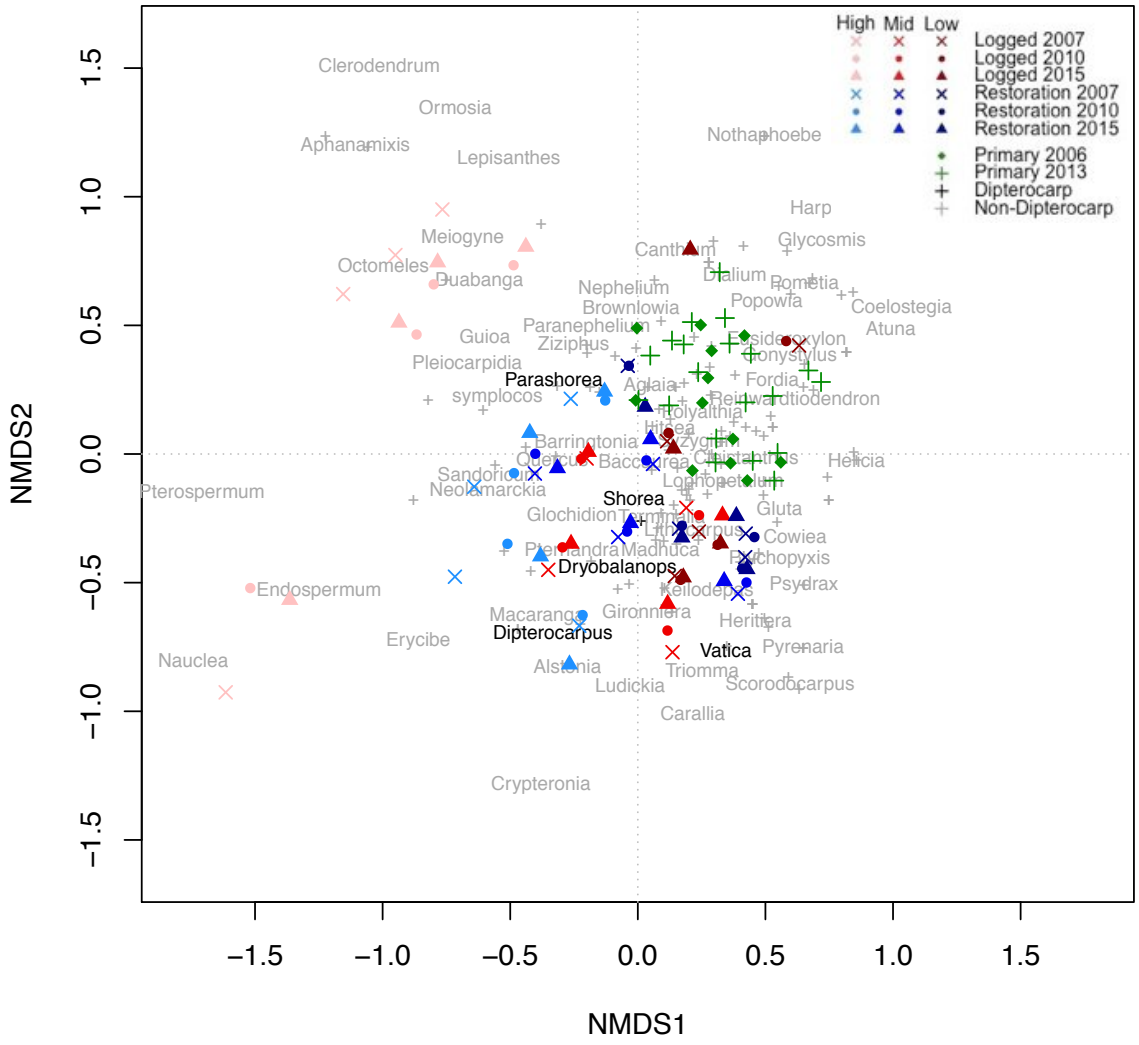

Figure 35. NMDS showing community composition of trees >10 cm DBH in sample plots and genus present in 2007, 2010 and 2015. Primary forest plots are shown in green, logged forest plots in red and restoration forest plots in blue. Logged and restoration plots are shaded from light to dark indicating logging intensity high to low. Genus in black are from the family Dipterocarpaceae, all other genus are in grey.

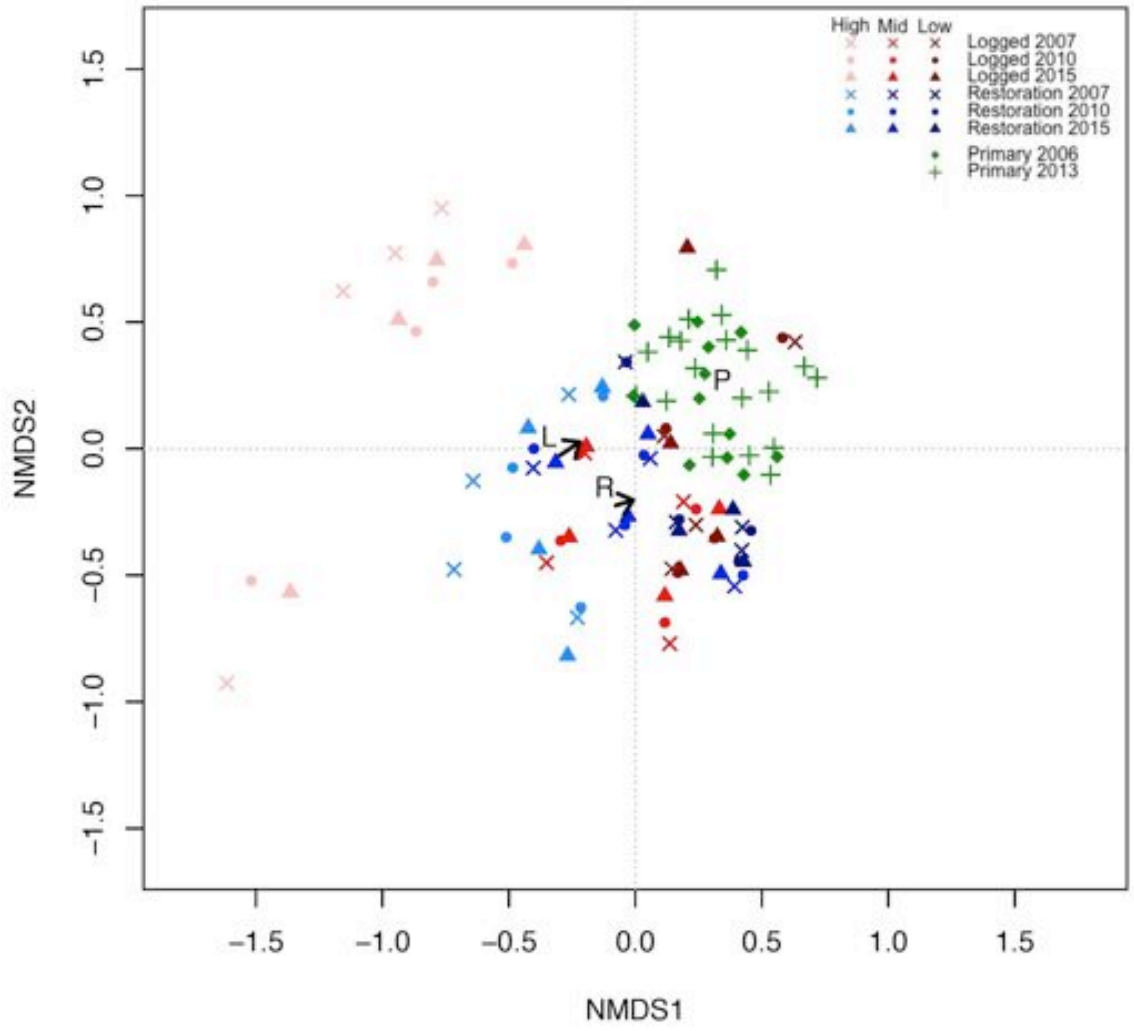

Figure 36. NMDS showing community composition of trees >10 cm DBH of plots in 2007, 2010 and 2015. Arrows show mean NMDS scores from census one (2007) to census three (2015) for logged forest (L) and restoration forest (R), and mean score for primary forest (P) in 2013. Primary forest plots are shown in green, logged forest plots in red and restoration forest plots in blue. Logged and restoration plots are shaded from light to dark indicating logging intensity high to low.

5.4.2. Causes of differences between logged and restoration forest

H1 - Forest were different prior to logging. The climate of the two treatments was identical, however, some differences in soil properties were observed. The C:N ratio was significantly higher in restoration plot, compared to both logged forest ($p = 0.004$) and primary forest ($p = 0.004$, Figure 37). Total extractable P was marginally lower in restoration forest than logged forest ($p = 0.07$).

Soil pH was slightly acidic in all forest types, with no significant differences among habitats (Figure 37). The effective Cation Exchange Capacity (eCEC) was also similar among logged, restoration and primary forest. However, in both restoration and primary forest, Al^{3+} was the most common cation, making up 89% and 82% of cations, respectively. Whereas, in logged forest, Al^{3+} made up just 21% of cations. Finally, the physical structure of soil was not significantly different among habitats (Figure 37).

Overall the higher total extractable P and lower Al^{3+} concentration in logged forest suggest it has slightly more fertile soil than restoration forest. However, despite having less fertile soil, restoration forest is accumulating AGB twice as fast as logged forest (Table 24) indicating that the restoration treatment is leading to faster forest recovery.

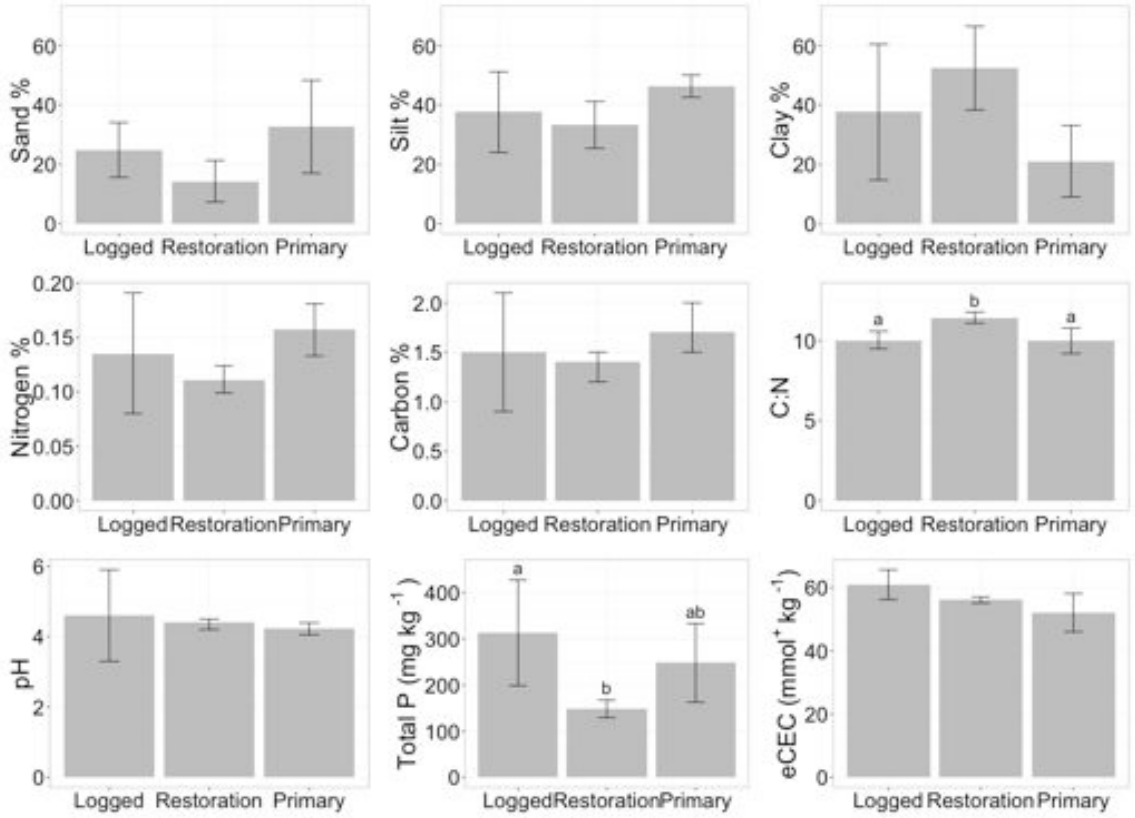

Figure 37. Soil physical and chemical properties in logged, restoration and primary forest between 0 and 30 cm depth Error bars show 95% CI. Letters denote significant differences (one-way ANOVA).

H2 – Forests allocated to restoration were logged differently. Given that environmental differences do not appear to be driving differences in the recovery of restoration compared to logged forest, there exists the possiblity that the forests experienced, on average, different logging levels prior to the restoration treatment. The total volume of timber extracted was significantly higher (T = -2.7, df = 17.2, p = 0.01), in restoration plots (98.3 m^3 ha^{-1}) compared to logged forest plots (58.4 m^3 ha^{-1}; Figure 38), because significantly more Red Seraya (T = -2.9, df = 17.9, p = 0.008) was extracted in restoration forest (48.8 m^3 ha^{-1}) than in logged forest (26.4 m^3 ha^{-1}, Figure 38). And significantly more Yellow Seraya (T = -2.6, df = 15, p = 0.02) extracted in restoration forest (3.5 m^3 ha^{-1}), than logged forest plots (1.3 m^3 ha^{-1} ; Figure 38). However, there was no significant difference in the percentage of total timber extracted between logged and restoration forest plots for all seven species groups (described in Table 23, Figure 39).

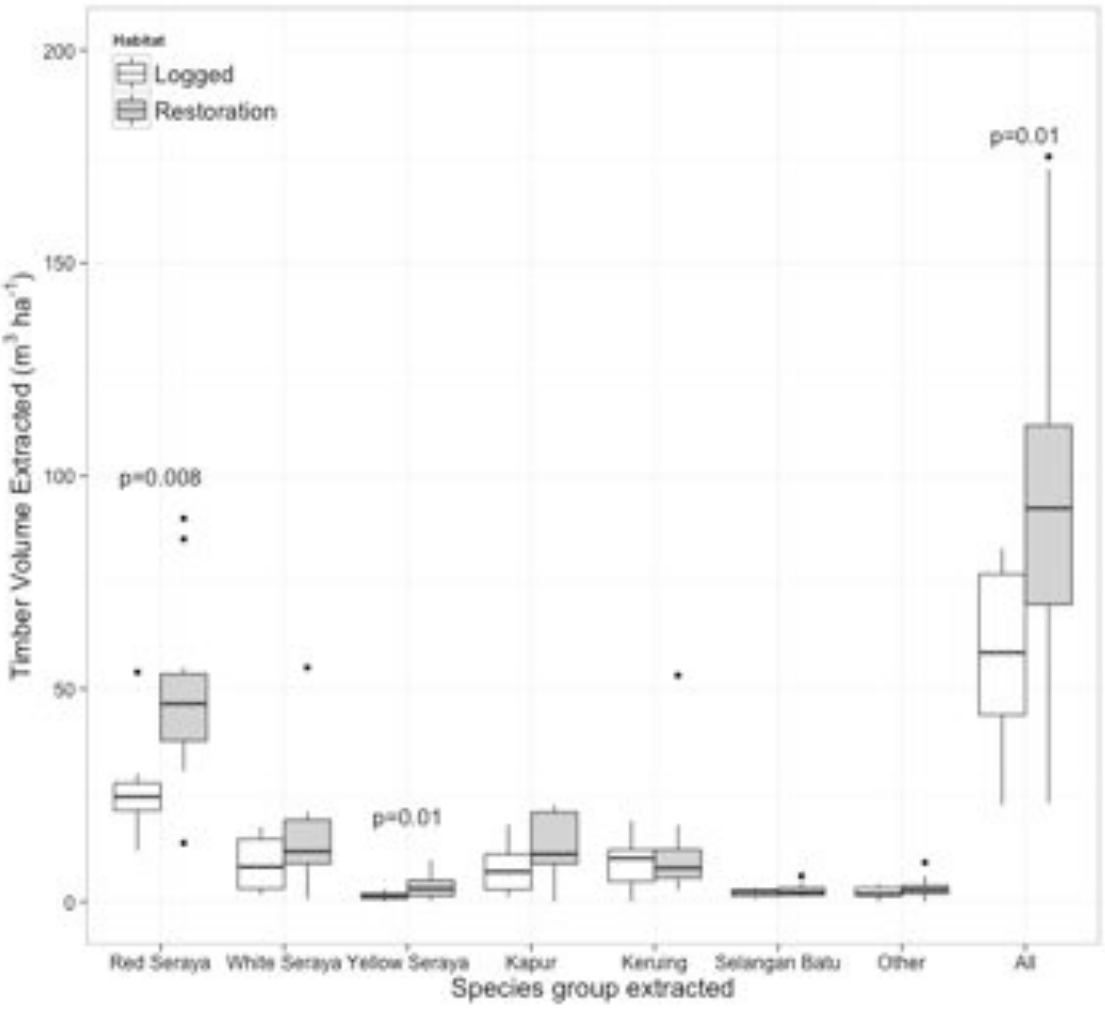

Figure 38. Boxplots showing total volume of timber extracted (m^3 ha^{-1}) for each species group in logged and restoration forest plots. Significant P values are shown.

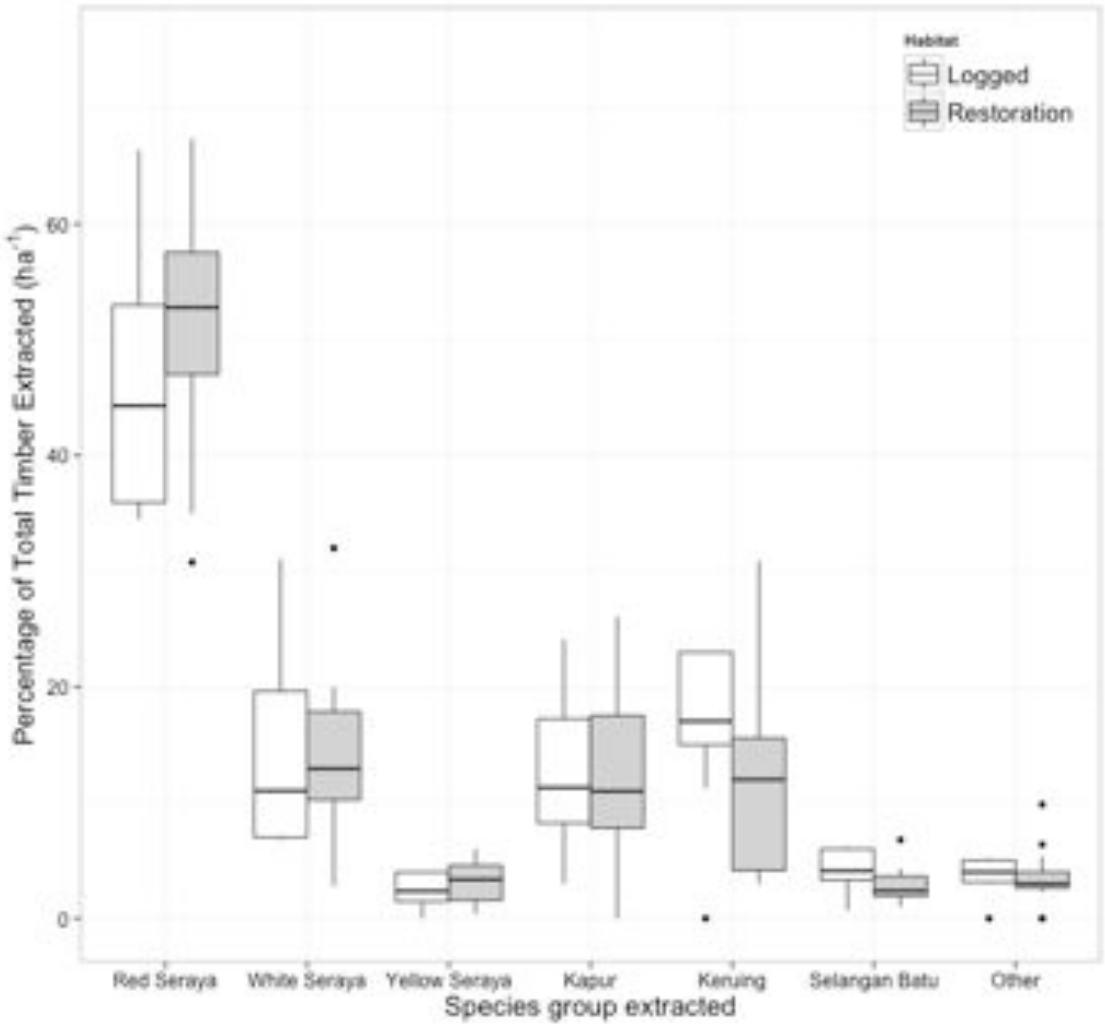

Figure 39. Boxplots showing percentage of total timber extracted (ha^{-1}) for each species group in logged and restoration forest plots.

H3 – Forest were different prior to restoration. Finally, results show that AGB accumulation was twice as fast in restoration forest compared to logged forest (Table 24). I tested to see if these differences were due to initial differences in forest structure or species composition between the logged and restoration areas prior to restoration treatment (i.e. in 2000), rather than due to the restoration treatment. From, PCA I produced two principal components; PC1 related to forest structure (AGB. BA, and stem density) and PC2 related to species composition (WD), which were used as covariates in two separate ANCOVAs.

Following model simplification ANCOVA showed that forest structure (PC1) in logged and restoration forest didn't differ significantly (T = 0.4, df = 20, p = 0.6). However, despite having similar structure, restoration forest accumulated significantly more AGB than logged forest (T = 2.7, df = 22, p = 0.01, Figure 40), with an AGB accumulation rate 3.6 Mg ha^{-1} yr^{-1} higher in restoration forest. Unlike forest structure, species composition (PC2) was significantly different between restoration and logged forest (T = 3.7, df = 21, p = 0.001). However, once these differences were controlled for restoration forest still had a significantly higher AGB accumulation rate than logged forest (T = 4.2, df = 21, p = <0.001, Figure 40), with an additional 4.6 Mg ha^{-1} yr^{-1} of AGB. These results suggest that the observed difference in AGB accumulation between logged and restoration forest were as a result of the restoration treatment and not an artefact caused by differences in site conditions.

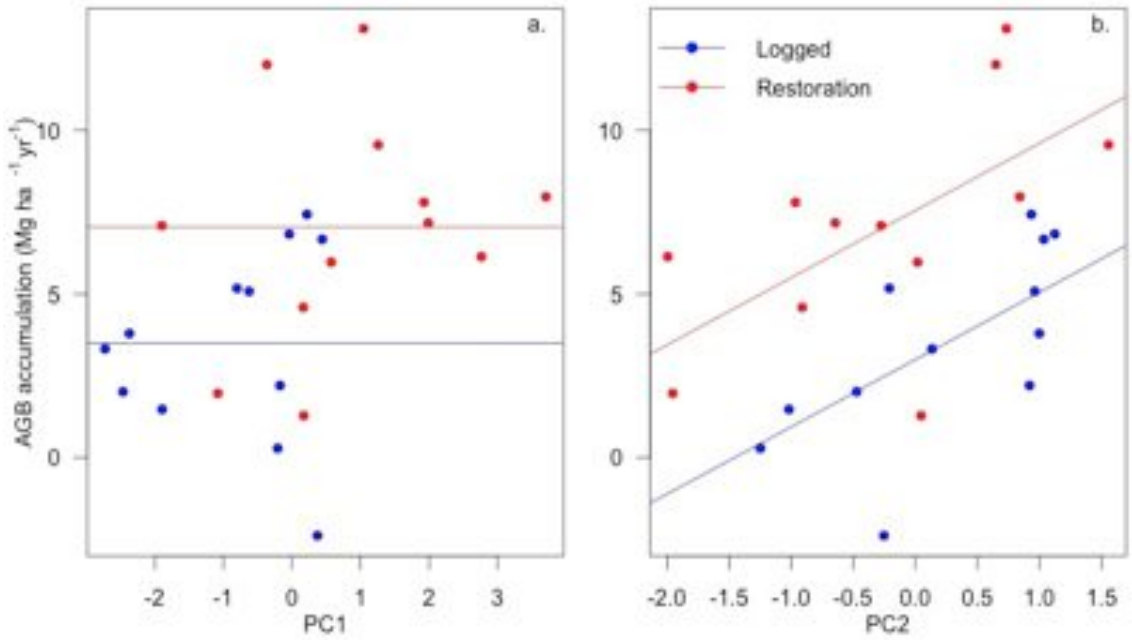

Figure 40. ANCOVA showing differences in AGB accumulation (Mg ha^{-1} yr^{-1}) between logged and restoration forest when controlling for a) PC1 (forest structure) and b) PC2 (species composition). Lines show the best fit linear model.

5.5. Discussion

5.5.1. Recovery of forest structure

These results show that restoration forest plots, that had been logged and then managed using a combination of climber cutting, planting with native seedlings and liberation thinning were recovering aboveground biomass (AGB) more than twice as fast as plots that were logged and left unmanaged (Table 24). A study by Berry et al. (2010) conducted in the same area as this study, estimated an AGB accumulation rate of 2.7 Mg ha^{-1} yr^{-1} over an 18 year timeframe, slightly lower than the AGB accumulation of 3.5 Mg ha^{-1} yr^{-1} estimated for logged forest in this study, and much lower than the 7.8 Mg ha^{-1} yr^{-1} estimated for restoration forest plots, suggesting that the restoration treatment is increasing the AGB accumulation rate expected in logged forest in this region. The AGWP in restoration plots was indistinguishable from primary forest at 10.7 Mg ha^{-1} yr^{-1}.and 10.9 Mg ha^{-1} yr^{-1} respectively, whereas logged forest was lower at 7.3 Mg ha^{-1} yr^{-1}. This is higher that observed by Talbot et al. (2014) and (Malhi et al., 2004), who estimated AGWP of 6.2 Mg ha^{-1} yr^{-1}, and 6.6 Mg ha^{-1} yr^{-1}, respectively. However these studies were both conducted in the Amazon, and therefore the slight difference in AGWP could be due to the slightly higher net primary productivity of Southeast Asian forest (Malhi, 2012).

By 2015, AGB was, on average, 95% of that seen in primary forest (Table 30), and if the current rate of AGB accumulation continued, restoration forest would reach primary forest AGB levels in just two more years. Unsurprisingly, there were differences given logging intensity prior to restoration: low intensity plots have exceeded primary forest AGB; medium intensity plots would take five more years to reach primary forest AGB; and even in high intensity restoration plots, it would take just another 29 years for forest to reach primary forest AGB (Table 30).

Whereas, logged forest plots had just 53% of primary forest AGB by 2015, and would require another 50 years to reach primary forest AGB. Of particular interest were high intensity logged forest plots, which by 2015 had just 22% of the AGB seen in primary

forest and a slow AGB accumulation rate of 2.5 Mg ha^{-1} yr^{-1}, meaning that it would take another 116 years for logged forest to attain primary forest AGB (Table 30).

This result could suggest that whilst mid and low intensity logged forest plots were recovering forest structure, albeit slower than restoration forest, that the high intensity areas were struggling to recover without any management interventions, therefore focusing restoration efforts on areas that have undergone heavy logging might be a more cost effective approach to management. Whilst there would be cost implication associated with conducting surveys to identify areas of high intensity logging, it is likely to still offer financial incentives, by reducing the area to be planted. Reducing the planting area would reduce the cost associated with: nursery propagation of seedlings, cutting of planting lines, planting of seedlings and tending of seedlings. As the costs of restoration were substantial, estimated at approximately $125 thousand ha^{-1} in the INFAPRO project (RM 5000 ha^{-1}, J.Abun personal communication), this is likely an attractive prospect.

Table 30. Rate of change for AGB (Mg ha^{-1} yr^{-1}), BA (m^3 ha^{-1} yr^{-1}) and Stem density (stems ha^{-1} yr^{-1}) in logged and restoration forest at high, mid and low intensity logging

		Logged			Restoration		
		Rate of change	Percent [a]	Years [b]	Rate of change	Percent [a]	Years [b]
AGB (Mg ha^{-1} yr^{-1})	High	2.5	22	116	5	61	29
	Mid	3.3	66	39	7.3	91	5
	Low	4.6	70	24	11.1	134	0
	Mean	3.5	53	50	7.8	95	2
BA (m^3 ha^{-1} yr^{-1})	High	0.4	41	41	0.5	92	4
	Mid	0.1	83	47	0.4	123	0
	Low	0.4	91	6	0.6	137	0
	Mean	0.3	72	26	0.5	117	0
Stem density (ha^{-1} yr^{-1})	High	13.2	77	7	10.8	108	0
	Mid	1.9	95	10	4.1	125	0
	Low	1.8	98	4	-0.8	116	0
	Mean	5.6	90	7	4.7	116	0

, *a* = percentage of primary forest AGB, BA or Stems attained by 2015, *b* = number of years to reach primary forest AGB, BA or stem density using predicted rate of change.

The AGB of primary forest (373.2 Mg ha^{-1} in 2013) and selectively logged forest (183.1 Mg ha^{-1} in 2015) estimated in this study falls within the range of five other studies conducted in DVCA and the surrounding selectively logged forest (Figure 41). The AGB in logged

forest ranged from 132.9 to 272.1 Mg ha^{-1} in forest that was logged between one and 26 years. When the two studies that were logged <20 years earlier were removed this range reduces to 183.1 to 272.1 Mg ha^{-1}, with this study at the lowest end of the spectrum. The AGB of low and mid intensity logging plots both fall within this range, whereas high intensity plots were much lower than seen in other studies. This suggests that either, high intensity logged plots have lower AGB than would be expected 26 years after logging. Or, that very heavily logged sites were under-represented in other studies.

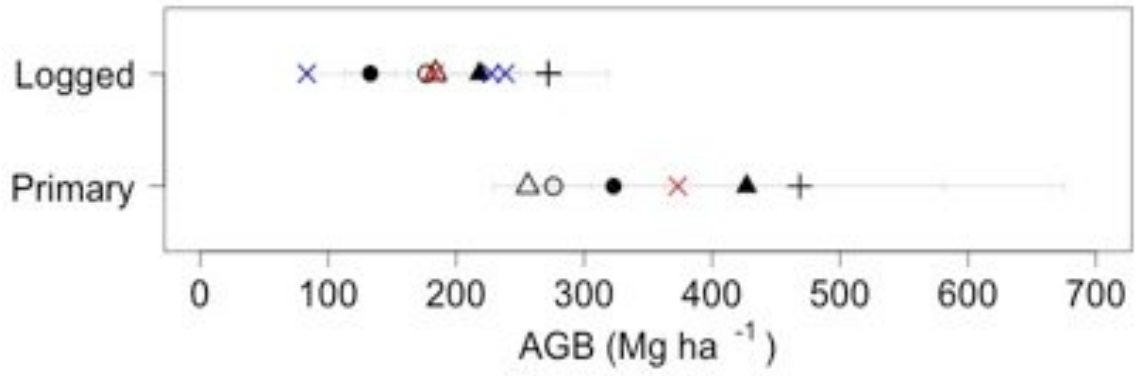

Figure 41. Multi-study Comparison of AGB in primary and logged forest in the Yayasan sabah forestry management area. Red cross = this study, 26 years after logging, blue crosses = this study (high, mid and low intensity plots from left to right), + = Hector et al. (2011) 26 years after logging, filled triangle = Tangki and Chappell (2008) mean 21 years after logging, filled circle = Pinard and Putz (1996) 1 year after logging, open triangle = Saner et al. (2012) 22 years after logging, open circle = Berry et al. (2010) 18 years after logging. Grey bars show 95% CI.

Whilst the AGB of primary and logged forest plots is typical of the local area it is unclear if the observed AGB in restoration forest is what would be expected, as studies measuring changes in selectively logged forest that has undergone restoration were rare. Indeed, this is the only study I am aware of that has assessed restoration in selectively logged forest over multiple censuses, for a duration of over ten years. Therefore this study, which measures changed in both forest structure and tree diversity over a 15-year time frame, offers new insights into the effect of active restoration in selectively logged forest.

5.5.2. Carbon storage in restoration forest

Between 1993 and 2006, a total of 11,440 ha of forest, underwent restoration management, within the INFAPRO project. This area stored a total of 2 Tg C (1 Teragram = 1 million Mg). This value was calculated by working backwards from a mean AGB of 355.5 Mg ha^{-1} (Table 25), measured following 11 years of recovery post-logging and 15 years of recovery post-restoration. Using the mean AGB accumulation rates of 3.5 Mg ha^{-1} yr^{-1} in logged forest and 7.8 Mg ha^{-1} yr^{-1} in restoration forest (Table 24), I estimate post-logging AGB of 200 Mg ha^{-1} (355.5–(11*3.5)-(15*7.8)=200). Using 200 Mg ha^{-1} as a baseline for post-logging AGB allowed total AGB in 2015 to be estimated for each compartment, this was then multiplied by 0.471 to convert AGB to carbon (Thomas and Martin, 2012) (see Appendix 7 for a breakdown of the amount of carbon storage per compartment).

However, estimated total carbon storage result must be taken with caution, the highly heterogeneous nature of selective logging means that the baseline AGB, post-logging would be highly variable; therefore, using a mean baseline of 200 Mg ha^{-1} can only give a broad approximation of total carbon storage within the INFAPRO project area. Furthermore, we do not know the proportion of land that has undergone high, mid, and low intensity logging. Using a mean value of 355.5 Mg ha^{-1} AGB, implicitly assumes that one-third of the total land area underwent high, mid, and low intensity logging, however this may not be the case. Having baseline data of forest AGB post-logging or post-restoration would enable me to gain a more robust understanding of the influence of restoration on forest recovery and carbon sequestration.

A more accurate approach therefore, may be to estimate carbon additionality as a result of restoration management. Carbon additionality refers to the additional carbon sequestered by a forest as a result of restoration, i.e. the difference between carbon sequestration in the business-as-usual scenario (here naturally regenerating logged forest) and carbon sequestration in restored forest, since the time of restoration (Angelsen, 2008). A total of 0.7 Tg C had been accumulated since restoration began, in the 11,440 ha of restoration forest (Calculated as; AGB accumulation [7.8 Mg ha^{-1} yr^{-1}] * years since restoration * area * 0.471). More than double the 0.3 Tg C that would have accumulated without restoration management (AGB accumulation [3.5 Mg ha^{-1} yr^{-1}] * years since restoration * area * 0.471; see Appendix 8 for a breakdown of the amount of carbon sequestered with and without

restoration per compartment). Understanding the additionality of carbon as a result of restoration activities is valuable information in determining the success of restoration activities and is a key point in the negotiations of REDD+ for determining how emissions reductions will be monitored (Pistorius, 2012, Angelsen, 2008).

However these results highlight the need for baseline data in future restoration projects. This is particularly pertinent in the light of the inclusion of REDD+ into the Paris climate change agreement (UNFCCC, 2015), which will no doubt increase the drive to restore tropical forest. However, if actual carbon sequestration benefits of such projects were to be estimated, accurate monitoring of restoration forest from the outset is essential.

5.5.3. Recovery of tree diversity

My results show that forest restoration is beneficial for tree (≥10 cm DBH) diversity, with significantly higher species richness than logged forest, and the same species richness as primary forest, however species composition is still markedly different. Similar high levels of tree diversity in selectively logged forest have been observed in Danum Valley, Bischoff et al. (2005) found no differences in tree species richness in eight and 13 year old secondary forest, but also observed large variation in species composition, as seen in my study. Such high levels of tree diversity, specifically in mid and low intensity plots, could possibly be attributed to the intermediate disturbance hypothesis (Connell, 1978), which states that intermediate levels of disturbance (such as seen in mid and low intensity plots) maximise species richness. Evidence supporting this theory, has been shown for tropical forests (Bongers et al., 2009), however it is highly dependent on spatial scale (Condit et al., 2002)

High diversity of other taxa has also been observed within the INFAPRO project in comparison to logged and primary forest. A study by Edwards et al. (2009) found that the restoration of logged forest resulted in the recovery of birds diversity to levels seen in primary forest. However they did note that there were some differences in the abundance of different bird feeding guilds, with frugivores reducing in abundance in restoration forest, whilst insectivores increased in abundance. Another study by Ansell et al. (2011) assess differences in species composition. As was the case in my study, they found that

there were still significant differences in the species composition among habitats with restoration forest being slightly more similar to logged forest than primary forest.

A third study by Edwards et al. (2012) assessed understory invertebrate abundance at the ordinal taxonomic level in the INFAPRO project. They found that there were significant differences in the abundance of invertebrate orders as well as differences in the abundance of invertebrates of different feeding guilds (including herbivores, carnivores and detritivores) among habitats. However the differences between primary and restoration forest were smaller than the differences between primary and logged forest. All three of these studies were conducted using the same sample transects, within areas that were logged in 1989 and planted in 1994-1995. Despite being conducted in areas that underwent restoration five years earlier than the locations used in my study, all the studies were carried out between 13 and 15 years after restoration representing a similar timeframe following restoration to my study.

The fact that similar changes to species richness and composition have been observed over multiple taxa suggests that even though restoration management focuses on improving the regeneration of trees through replanting and liberation cutting, it has a broader biodiversity benefit for other forest fauna. However, the recovery of tree diversity has been shown to be slower than the recovery of carbon stocks due to slow rates of stem turnover (Martin et al., 2013), therefore it would be likely to take a number of years for tree species composition to be similar to that seen in primary forest.

5.5.4. Impact of restoration treatment

It is clear that restoration forest is recovering back to an intact forest state in terms of structure (BA and stem density) and AGB more rapidly than logged forest and it is more diverse than logged forest. However, caution is required in attributing these observed differences to restoration management practices. While planting lines and liberation thinning evidence was abundant, surprisingly, I identified very few planted stems along planting lines. The lack of planted stems could be due to three factors: (1) No seedling was planted, as there was natural regeneration at the planting point, (2) No seedling was planted as the location was unsuitable (rocky/ stream etc.) or (3) The planted seedling

died. It is likely that a combination of these three factors is occurring, but the exact contributions were unknown, because at the time of restoration, INFAPRO did not record if seedling were planted at a given planting position, nor the reason why a location was not planted. The low encounter rate of planted seedlings within the restoration forest means that other aspects of management, which include climber cutting, cutting of planting lines and tending of naturally regenerating seedlings, were likely having a dominant impact on recovery. Better documentation of restoration treatments is essential in future work to better assess which part(s) of restoration management packages were important to high recovery rate outcomes.

It appears that restoration using climber cutting significantly reduces climber abundance and that this effect is persistent for many years. A study by Ansell et al. (2011) conducted within the IFAPRO project determined the presence of small (<5 cm diameter) and large (≥5 cm diameter) lianas. They found that the presence of large lianas decreases significantly from 61% in primary and logged forest to 9% in restoration forest, whilst presence of small lianas also decreased significantly from 85% and 94% in primary and logged forest respectively, to 44% in restoration areas. This study by Ansell et al. was conducted 15 years after restoration treatment, the same duration after restoration as the results presented in this chapter, showing that climber cutting of liana, is still evident many years later.

Reductions in climber abundance have been linked to increased dipterocarp seedling growth in the Sabah Biodiversity Experiment (SBE, Dzulkifli 2014), another restoration project located close to the INFAPRO project, which has used very similar restoration methods. In the SBE, Dzulkifli (2014) found that the growth of 16 Dipterocarp seedling species was on average 28% higher in areas that had undergone replanting and climber cutting, compared to areas that had just undergone replanting. These same 16 species also had a 56% higher AGB accumulation in areas that had received replanting and climber cutting compared to areas that were just replanted. This study was conducted over a 2.5 year time period and suggests that restoration management that involves climber cutting is an effective means of increasing growth in Dipterocarps. However, the short duration of this study means that climber cutting as a restoration management intervention deserves more research, to understand its longer-term impact on tree growth and AGB accumulation.

5.5.5. Impact of timber extraction on forest recovery

The overall volume of timber removed during logging was 82.4 m^3 ha^{-1}, however significantly more timber was removed from forest compartments that had undergone restoration treatments, at 98.3 m^3 ha^{-1}, than in compartment that were logged and not restored, at 58.4 m^3 ha^{-1}. A meta-analysis by Martin et al. (2015) that included 11 studies from South-East Asia, eight of which were from Sabah, assessed the impact of selective logging on forest structure and function. They estimated that the median volume of timber removed in South-east Asia was 115 m^3 ha^{-1} (interquartile range 78 – 150 m^3 ha^{-1}), which is in line with the timber extraction predicted in my results.

In this meta-analysis Martin et al. used linear mixed models to relate the volume of timber extracted firstly to the number of trees removed and secondly to estimate the residual damage to the remaining stand. Using this model I predict that in logged forest 6 trees ha^{-1} were removed compared to 10 in restoration forest. This level of timber removal is estimated to cause damage to 35% of the residual tree stems in logged forest and 45% in restoration forest. Despite having a higher volume of timber removed during logging in restoration forest, and a resulting higher proportion of damaged stems in the residual stand, total AGB in restoration forest in 2015 is significantly higher than in logged forest in 2015, indicating a higher rate of recovery in restoration forest. This is indeed the case, with a mean net increase in AGB between 2007 and 2015 of 7.8 Mg ha^{-1} yr^{-1} in restoration forest, more than twice as fast as logged forest increasing at 3.5 Mg ha^{-1} yr^{-1}. It would be expected that areas that had experienced lower timber extraction would be recovering more rapidly following logging, however this is not the case. Thus I conclude that the higher recovery in restoration forest is likely due to restoration management interventions, most likely climber cutting and repeated liberation thinning of targeted naturally regenerating seedlings, rather than planting of seedlings. This opens the possibility of less financially costly restoration treatments, including climber cutting and liberation thinning in place of nursery seedling propagation, seed collection and planting.

5.6. Conclusions

Restoration using a combination of climber cutting, enrichment planting and liberation cutting doubled AGB recovery and resulted in accelerated recovery of forest structure, and biodiversity in comparison to areas of logged forest. In some areas, AGB, BA, stem density and species richness has reached or surpassed primary forest levels, albeit with remaining large differences in species composition. These results suggest that this is an effective method for restoring selectively logged forest, offering good carbon sequestration and biodiversity protection benefits.

However, logged forest, that has been left to regenerate naturally, also recovered forest structure and is becoming more diverse, particularly in areas that were less intensively logged. Indeed only high intensity logged forest plots are struggling to recover with just 22% of primary forest AGB after 26 years of regeneration. This finding suggests that focussing restoration efforts in very heavily degraded areas may be a more prudent and efficient approach to restoration of selectively logged forest.

6. Assessment of differing forest restoration options on long-term carbon dioxide removal from the atmosphere

6.1. Abstract

Restoring degraded and deforested tropical lands to sequester carbon is widely considered to offer substantial climate change mitigation opportunities, if conducted at large spatial scales. Despite this assertion estimates of how much carbon could be sequestered from the atmosphere as a result of large-scale restoration are largely lacking. This is due to the many different land use types available for restoration, which have varying rates of carbon sequestration, coupled with limited quantification of the area to be restored under each land use type. For six different restoration land use types: regenerating degraded forest, regenerating abandoned agricultural land, rotational selective logging, timber plantations, oil palm plantations and agroforestry, I estimated carbon sequestration rates from published literature. These were then used to project the likely carbon storage for each land use over 100 years. To account for the occasional losses of carbon on the land as food and timber is harvested I calculated time-averaged carbon stocks, T_{av}, which ranged from 196.7 Mg ha^{-1} in regenerating degraded forest, to 47.4 Mg ha^{-1} in timber plantations of *Acacia* species. Then I used these carbon estimates to explore the climate benefits of restoring a 1 million ha (Mha) area, in a hypothesised economically marginal area of the tropics, that was initially half abandoned agricultural land, and half degraded forest, firstly, restoring all 1 Mha to (i) natural forest, or (ii) converting 1 Mha to oil palm, as under some definitions this would still be forests, and (iii) an intermediate mixed-use scenario, where degraded forest remained forest (half regenerating degraded forest, half rotational logging), and agricultural land becomes tree based agricultural land (agroforestry, timber and oil palm plantations). Restoration to natural forest removed 107 Mt C from the atmosphere over 100 years; palm oil released 9 Mt C and the mixed-use scenario was in between at 48 Mt C. Taking nitrous oxide emissions from fertiliser use into account caused the oil palm scenario to have an even more negative impact on climate change over the 100 year timeframe. Overall, restoration to natural forests offers greatest

carbon benefits, and from a climate perspective oil palm is a poor choice, as emissions from fertiliser use offset much of the carbon stored on the land. However, incorporating multiple land uses within the landscape can provide carbon benefits if carefully planned.

6.2. Introduction

The recent signing of the Paris Agreement states an ambition to keep global temperatures well below 2˚C above pre-industrial levels (UNFCCC, 2015), and to achieve net zero greenhouse gas (GHG) emissions in the second half of this century (UNFCCC, 2015), by balancing sources and sinks of GHG emissions (Tian et al., 2016). Given current and likely future GHG emissions, this implies that active management and technological innovations to remove CO_2 from the atmosphere will be needed (Friedlingstein et al., 2014). Furthermore, the agreement states that parties should strive to enhance sinks of GHGs, specifically mentioning the role of forest. The inclusion of forest in the Paris Agreement, alongside other international initiatives on forest protection and enhancement has meant that forest restoration has been gaining prominence within the international policy arena (Suding et al., 2015). These initiatives include the New York declaration on forest, which builds on the BONN challenge (The BONN Challenge, 2016), aiming to restore 350 Mha of forest by 2030 (UNFCCC, 2014), as well as Aichi biodiversity target 15 of the Convention on Biological Diversity, which aims to restore 15% of degraded ecosystems by 2020 (CBD, 2013). Together these initiatives set ambitious targets for forest restoration, which alongside the Paris Agreement, raised the importance and likelihood of major new forest restoration across many countries.

This focus on forest restoration raises important questions such as: How much carbon can we expect large-scale forest restoration to remove from the atmosphere? Approximately 50% of a trees mass is carbon (Thomas and Martin, 2012), therefore, converting low carbon density agricultural landscapes to high carbon storage forest landscapes, could contribute to negative carbon emissions (Mackey et al., 2013). However, to achieve large negative carbon emissions restoration must be conducted over large spatial scales.

The World Resource Institute (WRI) and the International Union for the Conservation of Nature (IUCN) recently estimated that there were approximately two billion ha of land suitable for restoration globally (Minnemeyer et al., 2011). The United Nations Environmental Program (UNEP), estimated that if all 350 Mha were restored to a natural forest state, then by 2030 carbon sequestration in restored forest could reach 1 Pg C yr^{-1} (UNEP, 2015). Another study by Arora and Montenegro (2011) estimated that if 50% of

the tropical land area currently under cultivation (270 Mha) were to afforested then approximately 50 Pg C would be sequestered between 2011 and 2100, at a rate of approximately 0.6 Pg C yr^{-1}, providing a reduction in global temperatures of 0.16 ˚C. This equates to approximately 0.7 Pg C yr^{-1} over the same 350 Mha area.

These estimates, whilst useful, rely on lands being restored back to an intact forest state, however, there are other land use options, aside from natural forest, that could be used for both economic income and to increase terrestrial carbon storage, including tree-base agricultural (TBA) systems such as timber plantations, oil palm plantations and agroforests. Such options offer carbon gains on agricultural land, however; they have lower carbon density than naturally regenerating forest (Ziegler et al., 2012). In real-world situations it is unlikely that vast areas of land will be restored back only to intact forest, rather it is more likely that multiple TBA systems will be integrated with areas of naturally regenerating forest, to gain a host of ecosystem services and financial flows from food and timber production, alongside carbon sequestration, water management and other services. This process is often termed forest landscape restoration (FLR), and has been proposed as a way of providing carbon sequestration in degraded and agricultural landscapes whilst allowing for sustainable development, the production of crops and the provision of multiple ecosystem services (Chazdon et al., 2015).

However, from a climate regulation perspective there are a number of issues that must be considered when planning restoration at the landscape scale, to ensure net negative carbon emissions. The following four key points influence the effectiveness of forest restoration activities and must be considered for FLR to be a success. Firstly, in areas available for restoration, the transition from one land use type to another will result in very different carbon outcomes (Ziegler et al., 2012). To ensure positive carbon outcomes, the land use type selected for restoration must allow for a transition from a lower carbon density to a higher carbon density. This is particularly important in degraded forest, such as selective logged areas which can have a high carbon density prior to any restoration interventions, of >100 Mg C ha^{-1} (e.g. Pinard and Putz, 1996).

Secondly, calculating time averaged carbon stocks (T_{av}), which is the average carbon storage over a defined time period, allows for direct comparison in carbon stocks between land use types to be made (Yang et al., 2016). This approach accounts for differences in

rotation length of timber plantations and differences in the start date of planting (Palm et al., 1999). However, the time period over which T_{av} is calculated matters and can present different land use types as more or less favourable in terms of their total carbon storage. This is particularly important when the rotation length of a timber plantation is less than the time period used to calculate T_{av} carbon stocks and can provide misleading results (Palm et al., 1999).

Thirdly, different land use strategies available for FLR may represent a compromise between rotation length and carbon sequestration rate. Selecting restoration strategies with the highest C sequestration rate may appear as the most logical solution to rapidly sequester large quantities of C. However, land use types with the highest carbon accumulation rate may not remove the greatest amount of carbon from the atmosphere over long timescales. A meta-analysis by Bonner et al. (2013) found that monoculture plantations had a significantly higher AGB accumulation rate (10.9 Mg ha^{-1} yr^{-1}) than naturally regenerating secondary forest (7.7 Mg ha^{-1} yr^{-1}). However, as timber plantations have an average rotation length of between 20 and 30 years (Diaz-Balteiro and Rodriguez, 2006) the majority of the carbon is release back into the atmosphere at regular intervals as typically, such timber is used in the paper and pulp industry, so is respired back to the atmosphere once these products decompose, which in usually a short time after production. By contract, the naturally regenerating forest represents a longer-term carbon store, with carbon being retained within woody biomass for many decades (Galbraith et al., 2013).

Finally, carbon dioxide is not the only important greenhouse gas associated with land use. The application of fertiliser leads to the release of nitrous oxide (N_2O), globally estimated at 2.2 Pg CO_2e yr^{-1} (1 Pg = 10^{15} g) in the tropics between 2000 and 2010 (Tian et al., 2016). Given that the Paris Agreement sets the objective of achieving net zero GHG emissions in the second half of this century, emissions from fertiliser use of any land cover change should be accounted for to obtain better estimate of the climate benefits of changes in land cover. Nitrous oxide emission range from negligible in natural forest restoration without fertiliser use, to very high releases in some intensive crops such as oil palm (Kusin et al., 2016). Therefore, for any carbon gains (sinks) due to restoration, any offsetting N_2O losses (sources) from fertilizer additions must be accounted for, by converting to common units of CO_2e, in order to fully understand the impact of landscape scale restoration on climate change mitigation.

To address these four points I determine the total carbon storage and T_{av} carbon storage over a 100 year timeframe for six different common land use options available for FLR, to answer the following questions 1) What is the impact of restoration land use type carbon storage? 2) How does the time period used to estimate T_{av} alter the perceived benefits of different land use options? 3) How does T_{av} carbon storage change in relation to carbon sequestration rate and rotation length and 4) What are the N_2O emissions associated with fertilizer application in the six land use options? Following on from this, using estimated T_{av} carbon storage values, I estimate the total carbon storage of a model one Mha restoration project, under different restoration scenarios, to understand how large or small the net climate benefits of landscape scale restoration are.

6.3. Methods

6.3.1. Carbon stocks and sequestration of under different land cover types

I undertook a literature search to identify tree dominated land cover types that have been proposed as suitable for landscape scale restoration (FLR) in the tropics (IUCN and WRI, 2014, Arora and Montenegro, 2011, Chazdon et al., 2016b, Budiharta et al., 2014). Searches identified six land use options 1) natural regeneration of degraded frost; 2) natural regeneration of abandoned agricultural land,; 3) rotational selective logging of native forest; 4) timber plantations; 5) agroforestry systems and 6) oil palm plantations. See section 2.3 for more details on restoration land use options.

Literature searches were carried out on the web of science database using a combination of the following search terms; forest* AND tropic* AND (carbon OR biomass OR AGB) AND (sequest* OR accumulate* OR recover* OR stor*) AND (degrade* OR Abandon* OR regenerat* OR logg*) OR (oil AND palm) OR (timber OR plantation OR eucalyptus OR acacia) OR (agroforest*), to find values for the rate of carbon sequestration (Mg C ha^{-1} yr^{-1}) for each land use and average rotation length (in years) in TBA systems only. Studies were included for analysis if they were; one of the seven identified land uses; quoted carbon sequestration or biomass accumulation rate (Mg C ha^{-1} yr^{-1}, or Mg dry mass ha^{-1} yr^{-1}; and stated the time period (in years) these rates were estimated over. If review studies were identified, which quoted carbon sequestration values taken from multiple studies, then carbon sequestration rates from these were used rather than individual studies (e.g. Poorter et al., 2016). If only AGB accumulation was reported, values were multiplied by 0.471 to convert them into carbon sequestration rates, as this is the average carbon content of tropical forest trees (Thomas and Martin, 2012). I estimated rates of carbon sequestration for each of Latin America, Africa and Southeast Asia for degraded forest rotational logging land uses due to the structural differences of primary forest (Banin et al., 2012, Feldpausch et al., 2011) and the large variation in timber extraction rates following selective logging among continents (Martin et al., 2015). However, for the TBA land use, I did not disagregate by continent, and present pan-topical carbon sequestration

rates, due to a limited number of studies, and for example, similar carbon stocks of oil palm regardless of which continent the plantation was on.

The individual studies adhering to my selection criteria reported linear rates of carbon sequestration over a defined time period. Yet tree growth and carbon sequestration is more likely to approximate an asymptotic function over time as the carbon stocks associated with the local environment or management regime is reached. I therefore modelled carbon sequestration using a 3-parameter asymptotic function of the form:

$y=a - b \exp^{(-cx)}$,

Where y = Aboveground carbon (AGC), x = year, and a, b and c are constants. a = asymptote, b = asymptote – intercept and c = Ln ((a-y)/b)/x, taking x and y values where the slope is steepest (Crawley, 2012).

Values for coefficients a, the asymptotic AGC value, and b, the asymptotic AGC values of coefficient c. For all land uses asymptotic AGC values were assumed to be the pan-tropical mean of primary forest (Table 31), except oil palm plantations, which used asymptotic AGC value from the literature for the AGC of a mature oil palm plantation (Table 31). Additionally, in degraded forest and rotational logging land uses, separate asymptotic AGC values were taken from the primary forest for each region (Latin America, Southeast Asia and Africa; Table 31). Intercept values were taken as follows: in timber plantations, agroforestry, oil palm and abandoned agricultural land uses, intercept = 0 Mg C ha^{-1}. In degraded forest and rotational logging, intercept = post logging AGC at year 1 (T_1). Calculated as follows;

$C_{postlog} = C_{initial} - C_{timber} - C_{damage} + C_{longtermstorage}$

Where $C_{postlog}$ = carbon stock post-logging, $C_{initial}$ = carbon in primary forest, C_{timber} = carbon content of extracted timber and C_{damage} = carbon content of damaged trees in the residual stand. For simplicity carbon emissions into the atmosphere from the decomposition of damaged trees were assumed to be instantaneous, however, timber has a half-life of 4.1 years, based on empirical measurements, before it is respired to the atmosphere (Chambers et al., 2000). $C_{longtermstorage}$ = carbon stored in long-term harvested wood products, which last >100 years, taken as 13.5% of the carbon content of extracted timber

(Winjum et al., 1998). These values of a and b were used to estimate the values of coefficient c for each land use, ensuring the same rate of carbon sequestration over the stated duration taken from the literature. The resulting non-linear models were used to estimate AGC values from 1 to 100 years after a change in land use.

Table 31. 3-Parameter Asymptotic exponential coefficients for all land use types.

		Coefficients				
Land Use type	Region	A	B	X	Y	C
Degraded forest	Latin America	149.9[1]	46.5	20	128	0.0376
	Africa	186.4[2]	45.7	20	165	0.0379
	South-east Asia	148.3[3]	83.3	20	91	0.0187
	Mean	184.0[1-3]	72.1	20	125	0.0100
Rotational selective logging	Latin America	149.9[1]	46.5	20	128	0.0376
	Africa	186.4[2]	45.7	20	165	0.0379
	South-east Asia	148.3[3]	83.3	20	91	0.0187
	Mean	184.0[1-3]	72.1	20	125	0.0100
Abandoned agricultural land		184.0[1-3]	184.0	25	83	0.0240
Eucalyptus plantation		184.0[1-3]	184.0	5	59	0.0773
Acacia plantation		184.0[1-3]	184.0	10	44	0.0273
Agroforestry		184.0[1-3]	184.0	5	23	0.0267
Oil palm plantation		63[4-8]	63	3	30	0.2155

1 = Baker et al. (2004a), 2 = Lewis et al. (2013), 3 = Slik et al. (2010), 4 = (Ng et al., 1968), 5 = Sanquetta et al. (2015), 6= Morel et al. (2012), 7 = van Noordwijk et al. (2010), 8 = Khalid et al. (1999)

In degraded forest and abandoned agricultural lands I assumed AGC increased over 100 years, with no removals of timber. In timber and oil palm plantations, which have a rotation period of <100 years, I assume that 100% of the carbon sequestered was emitted back into the atmosphere at the end of each rotation, then recovery begins again (see Figure 42). In agroforests, not all timber is harvested simultaneously, but rather tree cover is retained on the land. I assume that at the end of rotation one, 40% of the sequestered carbon was emitted back into the atmosphere (de Jong, 2001), the resulting value was then taken as the baseline carbon stock. In rotational logging land uses, I assume that AGC reduced to $C_{plogging}$ at the end of each rotation.

Carbon stocks were calculated in two ways. Firstly, carbon stock over a 100 year time horizon, from year one (T_1) to year 100 (T_{100}), were calculated using the non-linear models estimated for each land use types. Each of these values is the estimated carbon stored on

the land at that point in time. For locations where large areas are plantations, the value will be heavily dependent on where a given year is in the rotation cycle of the plantations. Therefore I also present a second method, time averaged (T_{av}) carbon stocks were calculated as:

$$\Sigma [T_1 + T_2 + ... T_{100}]/100$$

Where T_i = carbon stock for given year. Meaning T_{av} is the average carbon stock over the entire 100 year time horizon. T_{av} therefore accounts, on average, for both the carbon sequestered due to restoration activities and the carbon emitted following timber harvest (Figure 42). In both cases, either the stocks in a given year, or a longer T_{av} value, the carbon stock on the original land cover (T_0) must be subtracted to obtain the net change in stocks, and therefore the climate benefit.

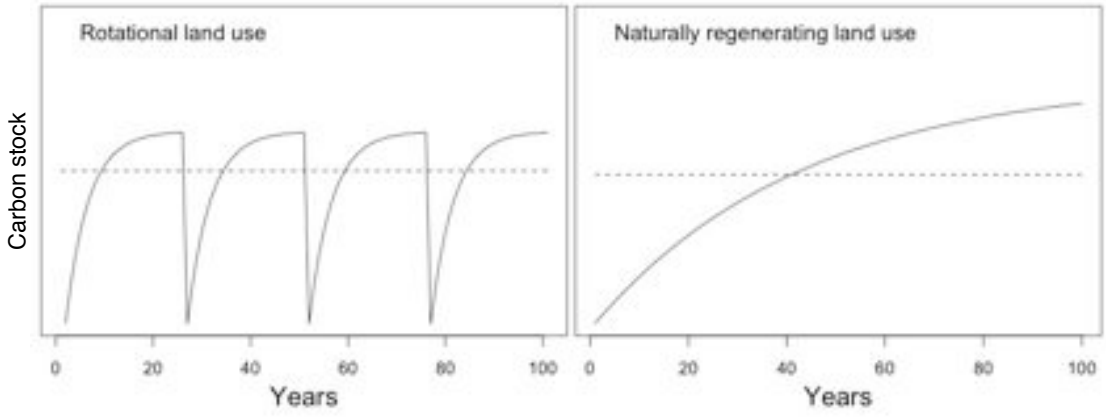

Figure 42. Diagram visualising how carbon stocks were calculated in rotational land uses (using a 25 year rotation as an example) and naturally regenerating land uses. Solid line shows carbon stocks at each year from T_1 to T_{100}. Dotted line shows T_{av} carbon.

In addition to carbon sequestration in AGC pools, carbon storage in belowground and necromass pools was calculated using published root: shoot ratios and live AGB: necromass ratios (Table 32) for each land use. I define necromass as standing or fallen coarse woody debris ≥10 cm diameter (Palace et al., 2012). In TBA systems a live AGB: necromass ratio of zero was used, as it was assumed that any necromass would be removed from very heavily managed timber plantations, and in agroforests, necromass would be removed for fuelwood. The additional carbon in belowground and necromass pools was added to the estimated values to give total carbon storage. Soil carbon storage

in restoration areas is likely to high, however, our understanding of soil carbon sequestration is limited, as are published values (Don et al., 2011), therefore I do not account for it in this chapter. Typically, soil carbon is positively related to the aboveground carbon, but more weakly in tropical systems. Nevertheless, any increase in carbon storage will likely be an underestimated as the soil organic carbon pool is not accounted for.

Table 32. Root: Shoot and Live AGB: Dead necromass ratios for all land use types.

Land Use type	Root: Shoot	Live mass: necromass
Primary forest	0.23 (± 0.06) [1-6]	0.13 (± 0.02) [15]
Degraded forest	0.23 (±0.06) [1-6]	0.13 (± 0.02) [15]
Rotational selective logging	0.23 (± 0.06) [1-6]	0.13 (± 0.02) [15]
Abandoned agricultural land	0.25 (± 0.14) [1,7]	0*
Eucalyptus plantation	0.24 (± 0.05) [8-12]	0*
Acacia plantation	0.20 (± 0.03) [12]	0*
Agroforestry	0.38 (± 0.03) [1,13]	0*
Oil palm plantation	0.22 (± 0.02) [1,14]	0*

95% CI in parenthesis. 1 = Yuen et al. (2013), 2 = Deans et al. (1996), 3 = Hertel et al. (2009), 4 = Phillips et al. (2008), 5 = Mokany et al. (2006), 6 = Niiyama et al. (2010), 7 = Fearnside and Guimarães (1996), 8 = Levillain et al. (2011), 9 = Werner and Murphy (2001), 10 = Fabião et al. (1995), 11 = Saint-André et al. (2005), 12 = Epron et al. (2013), 13 = Schroth et al. (2002), 14 = Corley et al. (1971), 15 = Palace et al. (2012). * Live mass: necromass ratio assumumed to be zero as necromass would beromoved from heavily managed plantations and extracted for fuelwood in agroforests.

6.3.2. Nitrous Oxide from fertiliser application emissions

N_2O emissions from fertiliser application were calculated. I assumed that 1% of fertiliser N was converted to N_2O, and then add the mass of the oxygen atoms (IPCC, 2006b):

$N_2O = N_2O\text{-}N \times (44/28) \equiv N_2O\text{-}N \times 1.57$ (IPCC, 2006b)

I.e. 1g N = 1.57g N_2O, and then express this as a standard 100 year global warming potential (GWP100) of 298, which includes climate-carbon feedbacks (IPCC, 2013) to convert N_2O emissions to CO_2 equivalent (CO_2e). A GWP100 was used, as this was consistent with the duration of projections for carbon sequestration within the different

FLR land uses. To calculate the net climate benefit of FLR land uses, I also convert carbon stocks into CO_{2e} using the equation:

$CO_2 = CO_2{-}C \times (44/12) \equiv CO_2{-}C \times 3.66$ (IPCC, 2006b)

I.e. 1g C = 3.66g CO_2. The net climate benefit is therefore, the additional carbon stored on the land minus the N_2O emissions, all expressed as $CO_{2e.}$

6.3.3. Scenario predictions

The carbon sequestration potential of landscape scale restoration was simulated using three different scenarios over a one Mha sample area. Land use at was assumed to be in a relatively remote location from markets for products, with 0.5 Mha of degraded forest and 0.5 Mha of recently abandoned agricultural land (T_0). The degraded forest areas were assumed to have a T_0 carbon stock (AGC + BGC + necromass) of 137.3 Mg C ha^{-1}, which is the mean post logging carbon stock of all three continents. The abandoned agricultural areas were assumed to have a T_0 carbon stock of 2.4 Mg C ha^{-1}, which is the mean AGC of plot in year 1 from data used in my systematic review (chapter 2). I estimated the net carbon benefit over 100 years using our estimated carbon stock values (Table 34). Net C benefit was defined as; carbon sequestration (in AGC, BGC and necromass) as a result of each of the scenarios of restoration, calculated as; T_{av} C stocks – T_0 C stocks.

In scenario one all 1 Mha were to restore back to intact forest. In scenario two all 1 Mha were converted to oil palm, as this is technically still a forest under FAO definition (FAO, 2000), and some may cynically consider this 'restoration'. An intermediate scenario, where existing forest remains as forests (half restoration to intact forest, half rotational logging), and the abandoned agricultural land becomes TBA (half agroforestry, a quarter timber plantation, a quarter palm oil), estimates what may occur in a real-world restoration landscapes.

6.4. Results

6.4.1. Carbon sequestration rates and time averaged carbon stocks

The carbon sequestration rates of different land use options are highly variable, with a mean carbon sequestration rate of 2.8 Mg ha^{-1} yr^{-1} (± 1.1; 95% CI), and ranging between 1.3 Mg ha^{-1} yr^{-1} in degraded forest and rotationally logged forest, to 7.4 Mg ha^{-1} yr^{-1} in *Eucalyptus* plantations (Table 33; Figure 43 - Figure 52).

Despite having the lowest rate of carbon sequestration compared to other land use options, degraded forests and rotationally logged forest have the two highest 100 year T_{av} carbon stocks at 197.2 Mg ha^{-1} (± 5.3) and 161.3 Mg ha^{-1} (± 3.2; Table 34, Figure 44, Figure 49, and Figure 53), or 70% and 57% of primary forest levels (280.7 Mg ha^{-1} ± 3.6, pan-tropical mean), respectively (Figure 43). Abandoned agricultural land has the third highest 100 year T_{av} carbon stock of 156.6 Mg ha^{-1} (± 12.8), or 56% of that observed in primary forest (Table 34).

These three land use options with the highest 100 year T_{av} carbon stocks are all naturally regenerating systems, recovering back to intact forest, with the exception of rotationally logged forest, which allows for extraction of timber resources. All tree based agriculture land use options have lower 100 year T_{av} carbon stocks than naturally regenerating land use options, with the highest found in *Eucalyptus* plantations (107.3 Mg ha^{-1} ± 10.2, Figure 50, Table 34) and the lowest in *Acacia* plantations (47.4 Mg ha^{-1} ± 5.4; based on a 20 year rotation length, Figure 50, Table 34). However, on average tree based agriculture land use options have higher carbon sequestration rates than naturally regenerating land use options (Table 33). This suggests that despite having higher rates of carbon sequestration, TBA systems do not attain high 100 year T_{av} carbon stocks, due to harvesting of food, wood and other products at the end of each rotation period, which for short-term products (food, paper, pulp), quickly returns to the atmosphere.

Table 33. Carbon sequestration rates, rotation length and duration of study for all land use types.

Land Use type	Region	Sequestration rate (Mg C ha^{-1} yr^{-1})	Rotation length (yrs)	Study length (yrs)
Primary forest	Latin America	0.28 [1]	NA	
	Africa	0.63 [2]	NA	
	South-east Asia	0.49 [2]	NA	
	Pan-tropical	0.47	NA	
Degraded forest	Latin America	1 [3,4]	NA	16 [3,4]
	Africa	2.4 [5]	NA	24 [5]
	South-east Asia	1.3 [6]	NA	18 [6]
	Pan-tropical	1.3	NA	
Rotational selective logging	Latin America	1 [3,4]	30 [23]	16 [3,4]
	Africa	2.4 [5]	30 [23]	24 [5]
	South-east Asia	1.3 [6]	30 [23]	18 [6]
	Pan-tropical	1.3	30	
Abandoned agricultural land		3.0 (0.6) [7,8,9]	0	22 [7,8,9]
Eucalyptus plantation		7.4 (3.7) [10,11]	20 [24]	20 [10,11]
Acacia plantation		3.9 (1.0) [10,12]	20 [24]	20 [10,12]
Agroforestry		4.4 (1.2) [13-16]	10 [13-16]	
Oil palm plantation		2.6 (1.1) [17-22]	25 [25]	25 [17-22]

95% CI in parenthesis. . 1 = Brienen et al. (2015), 2 = Lewis et al. (2009), 3 = Mazzei et al. (2010), 4 = West et al. (2014), 5 = Gourlet-Fleury et al. (2013), 6 = Berry et al. (2010), 7 = Bonner et al. (2013), 8 = Poorter et al. (2016), 9 = Carbon sequestration rate from model 2c from chapter 2 (short-term sites), 10 = Bouillet et al. (2013), 11 = Stape et al. (2010), 12 = Sang et al. (2013), 13 = Oelbermann et al. (2004), 14 = Kumar and Nair (2011), 15 = Nair et al. (2009), 16 = Kürsten and Burschel (1993), 16 = Corley et al. (1971), 17 = Ng et al. (1968), 19 = Sanquetta et al. (2015), 20 = Morel et al. (2012), 21 = van Noordwijk et al. (2010), 22 = Khalid et al. (1999), 23 = Putz et al. (2012), 24 = Diaz-Balteiro and Rodriguez (2006), 25 = Corley and Tinker (2008).

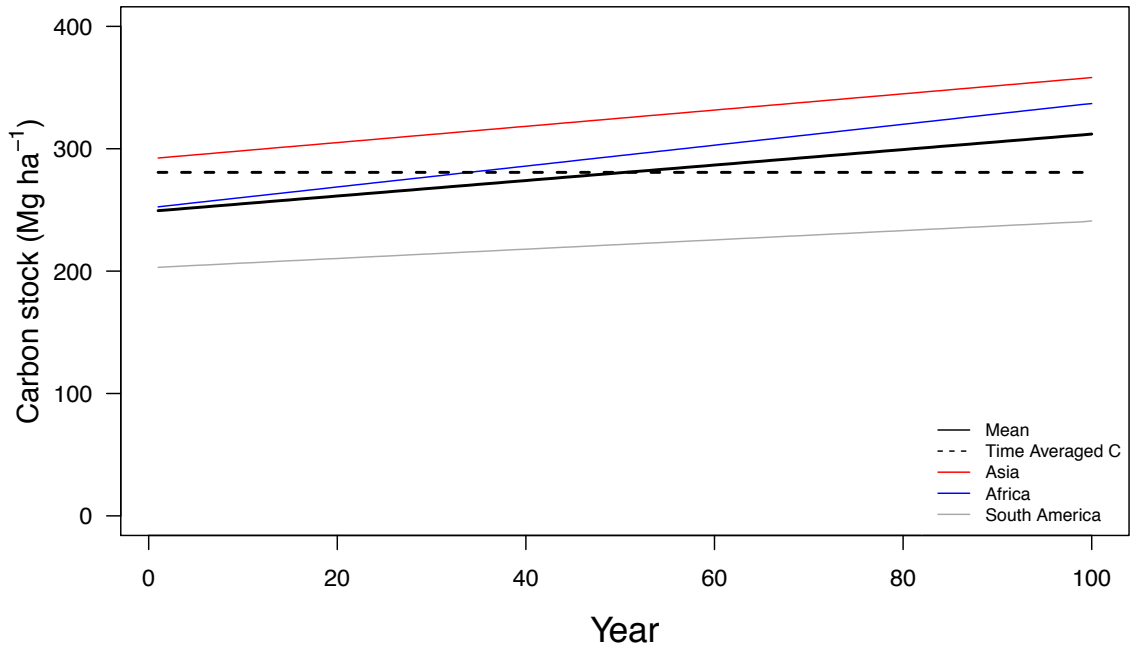

Figure 43. Change in estimated C stocks in Primary forest (n=3) over 100 years, seperated by region.

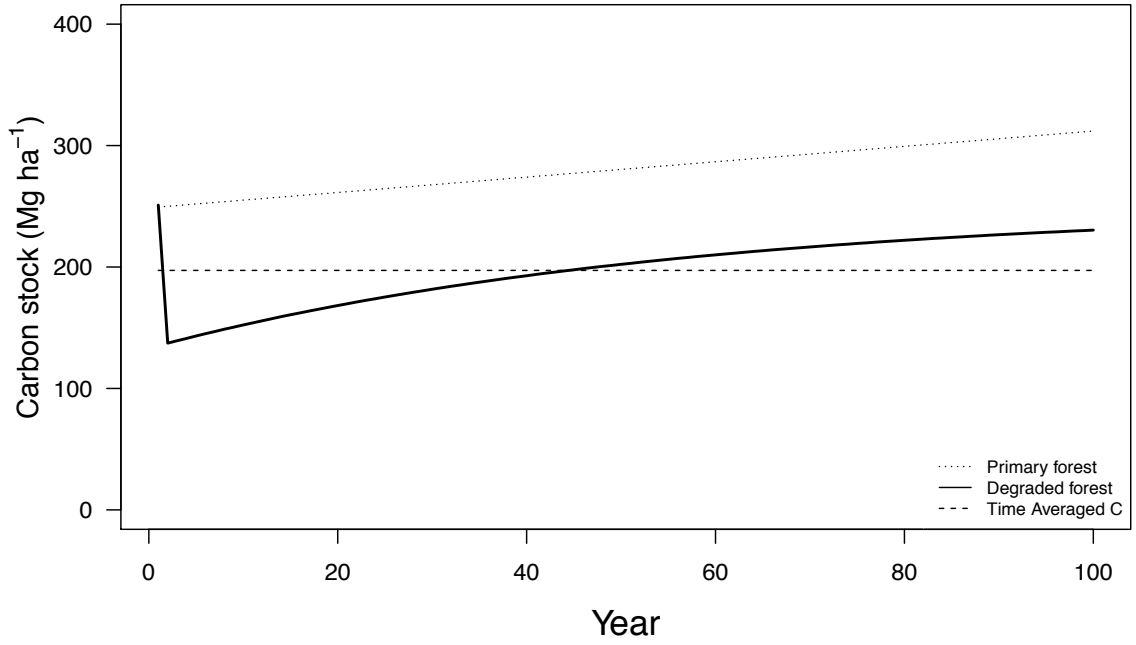

Figure 44. Pan-tropical change in estimated C stocks in degraded (selectively logged) forest (n=3) over 100 years.

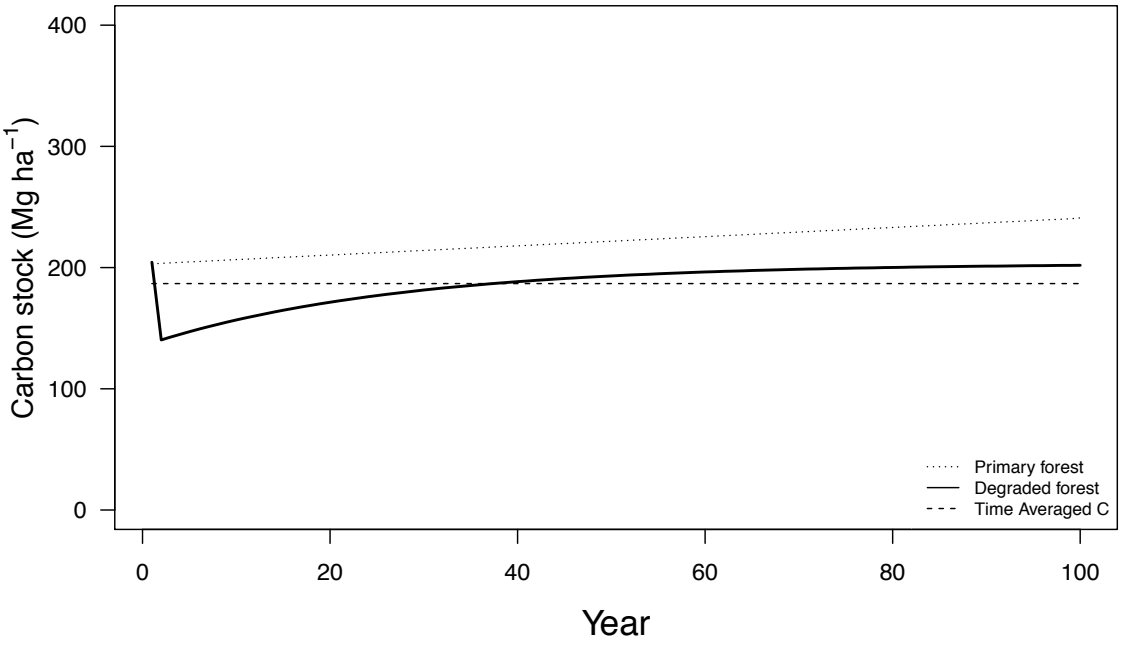

Figure 45. Change in estimated C stocks in degraded forest in South America (n=4) over 100 years.

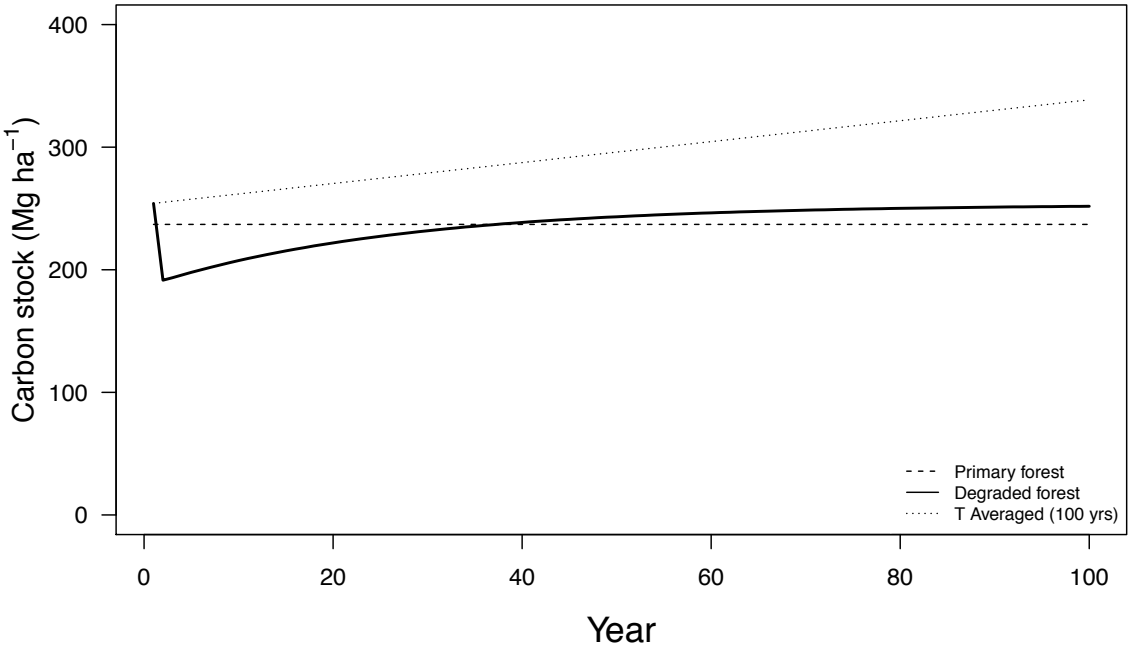

Figure 46. Change in estimated C stocks in degraded forest in Africa (n=2) over 100 years.

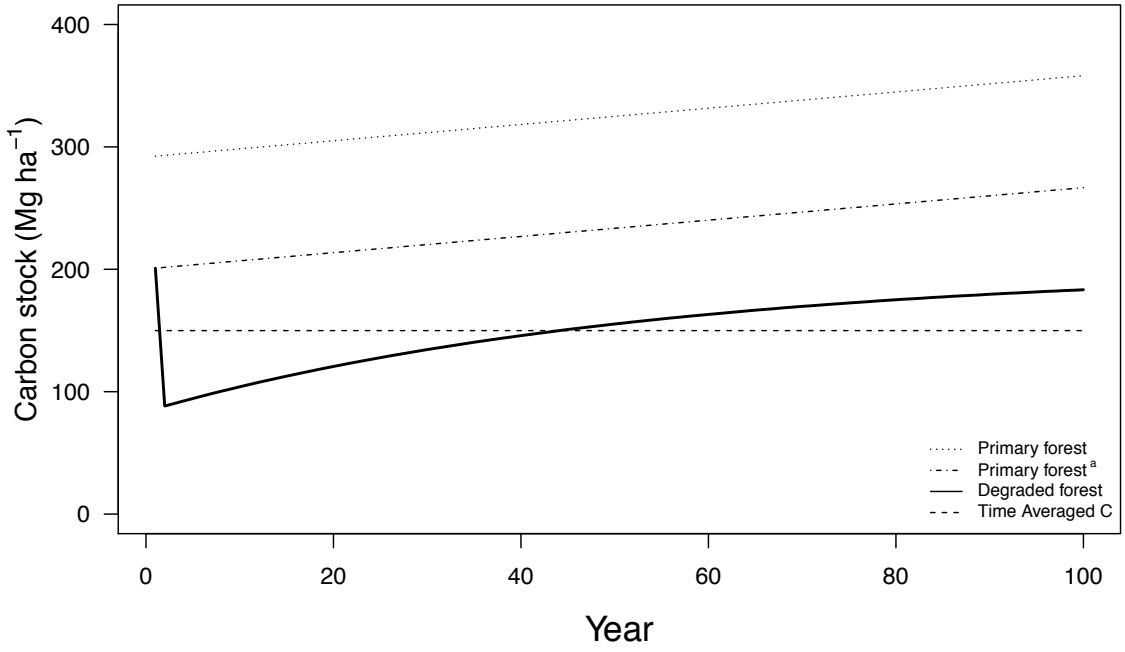

Figure 47. Change in estimated C stocks in degraded forest in Southeast Asia (n=4)over 100 years. Primary forest (dotted line) = T_0 AGC from Slik et al. (2010), Primary forest [a] (dot dash line) = T_0 AGC mean of Berry et al. (2010), Pinard and Putz (1996), Saner et al. (2012) and Tangki and Chappell (2008).

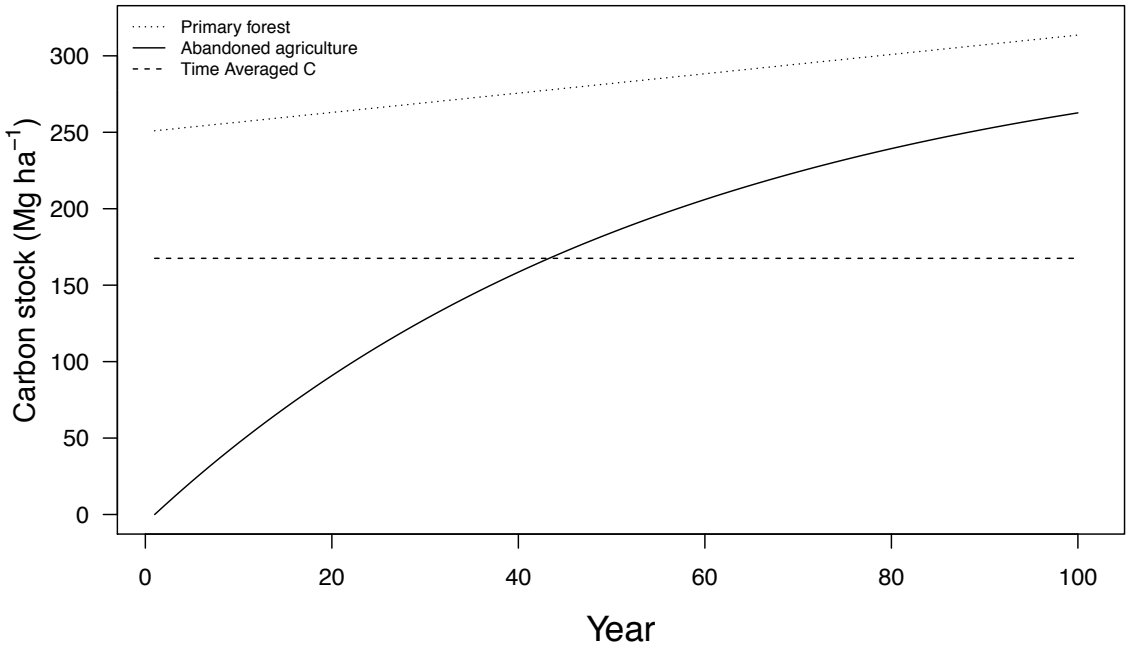

Figure 48. Change in estimated C stocks in abandoned agricultural land (n=2) over 100 years.

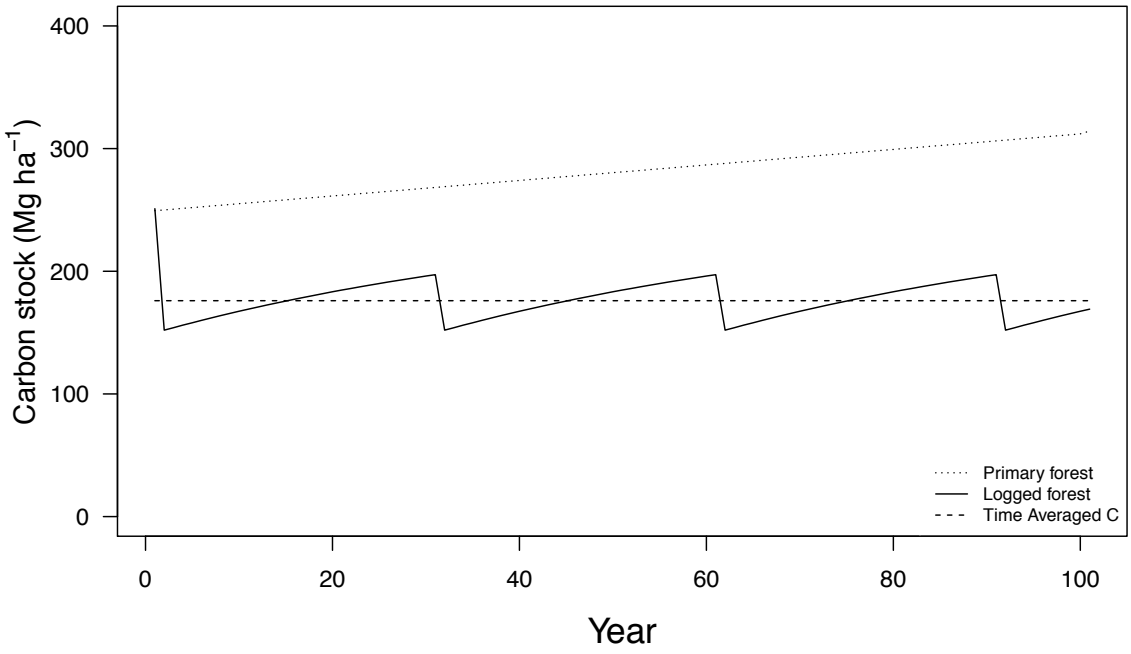

Figure 49. Change in estimated C stocks in rotationally logged forest (pan-tropical mean, n=3)), over 100 years,

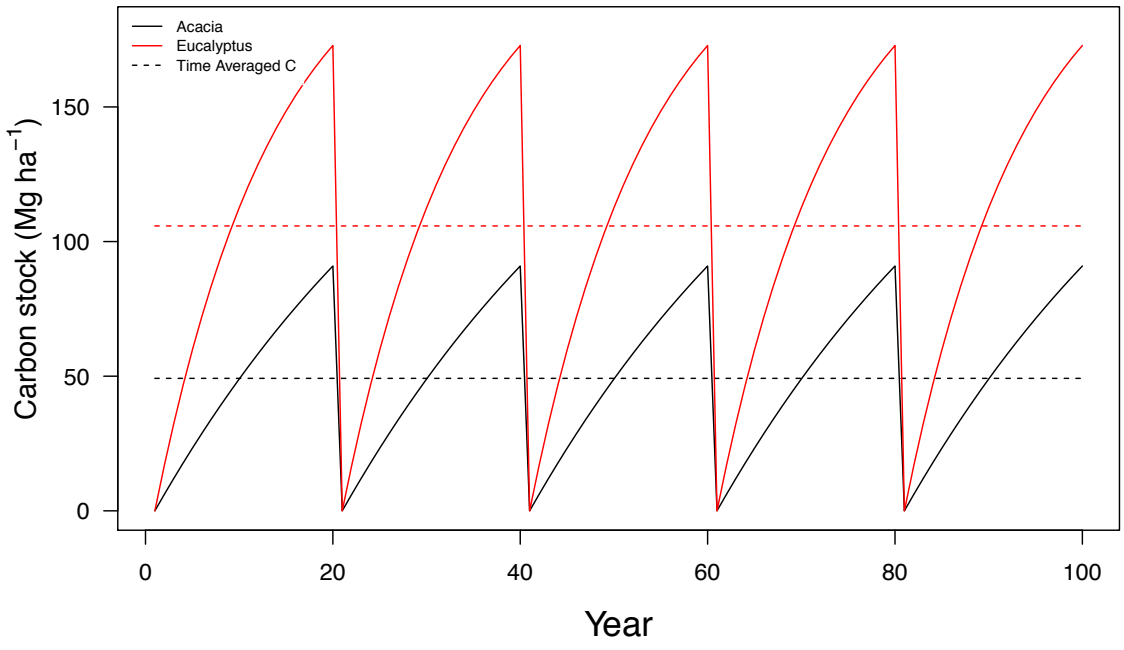

Figure 50. Change in estimated C stocks in Eucalyptus (n=2) and Acacia (n=2) plantations over 100 years.

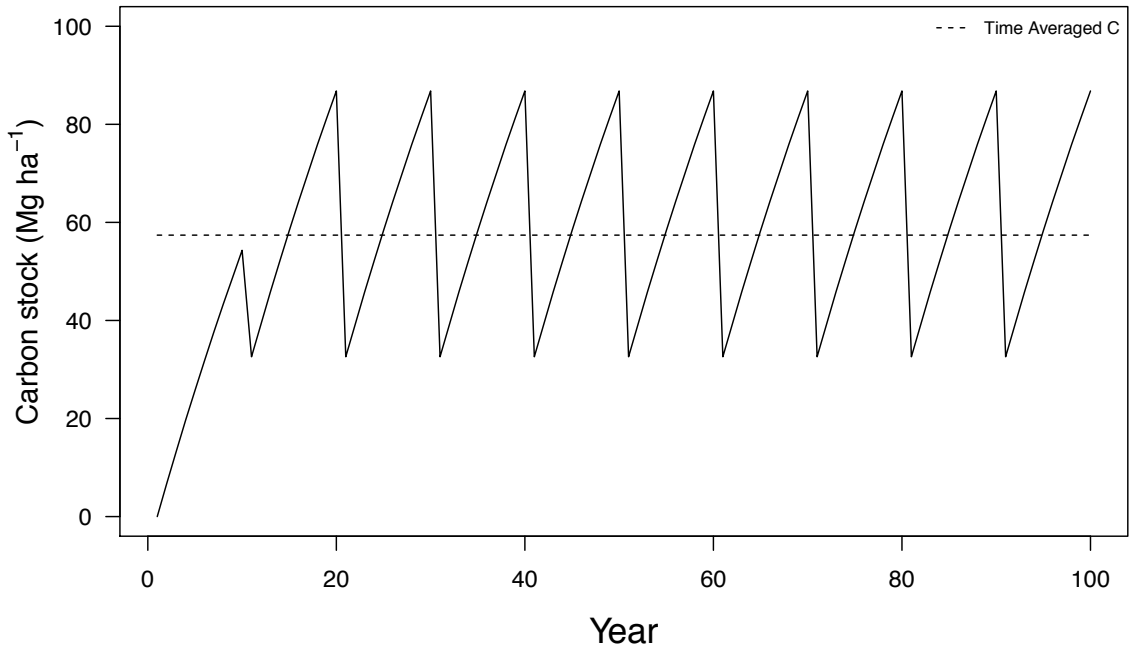

Figure 51. Change in estimated C stocks in agroforests (n=4) over 100 years, based on a ten year rotation length.

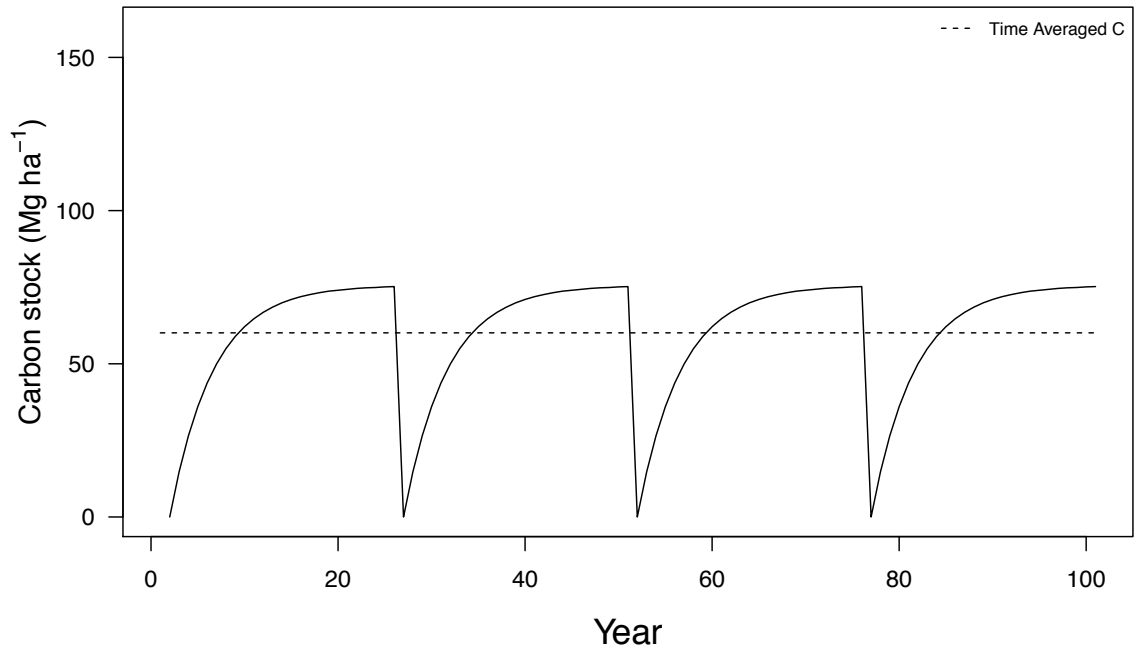

Figure 52. Change in estimated C stocks in palm oil plantations (n=6), planted on abandoned agricultural land over 100 years.

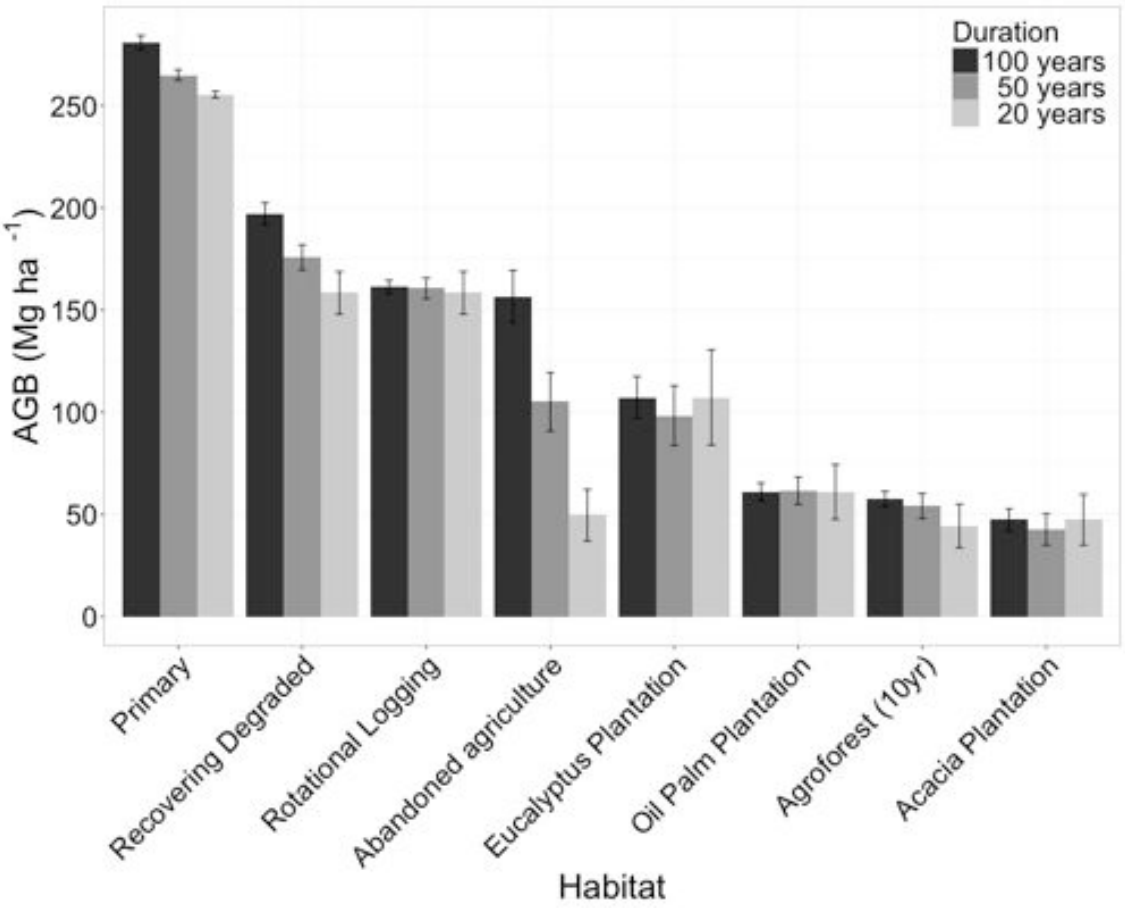

Figure 53. Time average carbon stocks using a projection period of 20,50 and 100 years for each land use option.

6.4.2. Influent of T_0 carbon stocks on total carbon storage

Carbon stocks prior to restoration have a large impact on net carbon stocks. In degraded forests that have undergone selective logging, C increases by 93.1 Mg ha^{-1} over 100 years, from 137.3 (± 58.4) Mg ha^{-1} immediately post logging, to 230.4 (± 40.1) Mg ha^{-1} (Pan-tropical mean, Figure 44, Table 34), giving a T_{av} carbon stock of 197.2 Mg ha^{-1}. However, if degraded land were to be converted into an intensive form of TBA, for example oil palm, C stocks would almost halve over 100 years, from 137.3 (± 58.4) Mg ha^{-1}, to 75.1 Mg ha^{-1} (Table 34). Furthermore, the T_{av} carbon stock would be 136 Mg ha^{-1} lower in a degraded forest that was converted to oil palm, than if it was left to recover back to intact forest.

Conversely, if oil palm plantations were located on abandoned agricultural land, which has an initial C stock of close to zero, they could offer carbon gains, with a 100 year time averaged C stock of 60.8 Mg ha^{-1} (± 4.3; Figure 52, Figure 53). However, if abandoned

agricultural land were allowed to naturally regenerate back to intact forest, carbon storage would increase (Figure 48, Table 34), with a time averaged C stock of 156.6 Mg ha^{-1} (Figure 53), 95.8 Mg ha^{-1} greater than in oil palm plantations. Tree-based agriculture land use options on abandoned agricultural land, lead to increased T_{av} carbon storage, than if areas were retained as agricultural land, however, if abandoned agricultural land were left to naturally regenerate, T_{av} carbon would be higher, as none of the TBA land uses has a higher time averaged carbon stock than naturally regenerating land (Figure 53).

Table 34. Carbon storage (AGC, BGC and necromass, Mg C ha^{-1}) at year 0, year 1 and year 100, and 100 year T_{av} carbon stocks for primary forest and all FLR land use options. a = year 1 values in degraded forest represent carbon stock immediately following logging.

		Year 0				Year 1 [a]				Year 100				T_{av}
Land Use type	Region	AGB	BGB	CWD	TAGB	AGB	BGB	CWD	TAGB	AGB	BGB	CWD	TAGB	(100yr)
Primary forest	Latin America	149.9	34.5	18.7	203.1					177.8	40.9	22.3	241.7	221.9
	Africa	186.4	42.9	23.3	252.5					248.6	57.2	31.1	337.5	294.8
	South-east Asia	215.8	49.6	27.0	292.4					264.8	60.8	33.1	358.8	325.3
	Pan-tropical	184.0	42.3	23.0	249.4					230.8	53.0	28.8	312.7	280.7
Degraded forest	Latin America	149.9	34.5	18.7	203.1	103.6	23.8	12.9	140.3	149.0	34.3	18.6	201.9	186.6
	Africa	186.4	42.9	23.3	252.5	141.3	32.5	17.7	191.5	185.8	42.7	23.2	251.8	236.8
	South-east Asia	215.8	49.6	27.0	292.4	65.1	15.0	8.1	88.3	135.3	31.1	16.9	183.3	149.4
	Pan-tropical	184.0	42.3	23.0	249.4	101.3	23.3	12.7	137.3	170.0	39.1	21.3	230.4	196.7
Rotational selective logging	Latin America	149.9	34.5	18.7	203.1	103.6	23.8	12.9	140.3	133.9	30.8	16.7	181.5	163.8
	Africa	186.4	42.9	23.3	252.5	141.3	32.5	17.7	191.5	171.1	39.4	21.4	231.8	214.4
	South-east Asia	215.8	49.6	27.0	292.4	65.1	15.0	8.1	88.3	99.2	22.8	12.4	134.4	113.2
	Pan-tropical	184.0	42.3	23.0	249.4	101.3	23.3	12.7	137.3	134.1	30.8	16.8	181.7	161.3
Abandoned agricultural land		-	-	-	-					168.0	42.0	21.0	230.9	156.6
Eucalyptus plantation		-	-	-	-					141.7	31.2	-	172.9	107.3
Acacia plantation		-	-	-	-					74.5	16.4	-	90.9	47.4
Agroforestry		-	-	-	-					62.9	23.9	-	86.8	48.1
Oil palm plantation (Agricultural land)		-	-	-	-					62.6	12.5	-	75.2	60.1

6.4.3. Duration of carbon projections

Using T_{av} carbon stocks enables a better comparison of the carbon benefit of different land uses by averaging over these rotation cycles. However, the time period over which T_{av} carbon stocks are calculated inevitably alters carbon stock estimates. In naturally regenerating land uses, which on average have continuous carbon sequestration until an asymptote, using a short time period to calculate T_{av} carbon stocks produces lower values (Figure 53). For example in abandoned agricultural land, over 20 year T_{av} carbon stocks were just 49.6 Mg ha^{-1}, where as, over 100 years T_{av} carbon stocks were over 100 Mg C ha^{-1} higher, at 156.6 Mg C ha^{-1} (Figure 53). In other land cover types, differences between 20, 50 and 100 years are much less marked (Figure 53). However, in TBA land uses, when the time period used to calculate T_{av} carbon stocks is less than the rotation length a misleadingly large value of carbon stocks is given as the losses of carbon upon rotation are missed. For example, in *Eucalyptus* plantations, 20 year T_{av} carbon stocks are 107.3 Mg C ha^{-1}, higher than 50 year T_{av} carbon stock at 98.4 Mg C ha^{-1} (Figure 53), due to 20 year T_{av} carbon stock coinciding with the end of a rotation period, whilst 50 year T_{av} carbon stock are halfway through a rotation.

6.4.4. Carbon sequestration rate verses rotation length

Land use options that have a low rate of carbon sequestration coupled with a long rotation length, for example, rotational logging, can have higher time averaged carbon storage than land use options with a high carbon sequestration rate coupled with a short rotation length, for example *Eucalyptus* plantations (Figure 53). Rotational logging forest have a 100 year T_{av} carbon stock 89.4 Mg C ha^{-1} higher than *Eucalyptus* plantations (Figure 53), despite having a carbon sequestration rate 5.7 times slower (Table 33), partly due to carbon being stored in the forest system for a much longer time period.

6.4.5. Nitrous oxide emissions from fertilisers

In TBA systems, oil palm plantations have by far the highest application of nitrogen fertiliser, with an average application rate of 100 kg ha^{-1} yr^{-1} (Kusin et al., 2016), emitting

0.16 Mg ha^{-1} of N_2O over a 100 year time period, equivalent to 46.8 Mg CO_2e ha^{-1}. The 100 year T_{av} carbon stock of oil palm plantations is 220.0 Mg CO_2e ha^{-1} (60.1 Mg C ha^{-1}), thus, the net climate benefit of oil palm plantations is 173.1 Mg CO_2e ha^{-1} (net climate benefit = 220-46.8) over a 100 year time period. For timber plantations, nitrogen fertiliser application rates are lower (FAO, 1993, CIFOR, 2004) and only once per rotation. In *Eucalyptus* plantations an average of 47.1 (± 19.1) kg ha^{-1} yr^{-1} of fertiliser is added at the time of planting (FAO, 1993, CIFOR, 2004), emitting 0.004 Mg ha^{-1} of N_2O over a 100 year time period, equivalent to 1.1 Mg CO_2e ha^{-1}. The T_{av} CO_2 stock of *Eucalyptus* plantations is 392.6 Mg CO_2e ha^{-1} (107.3 Mg C ha^{-1}), thus, the net climate benefit of *Eucalyptus* plantations is 391.5 Mg CO_2e ha^{-1} over a 100 year time period. In *Acacia* plantations an average of 20.7 (± 19.1) kg ha^{-1} yr^{-1} of fertiliser is added at the time of planting (FAO, 1993, CIFOR, 2004), emitting 0.002 Mg ha^{-1} of N_2O over a 100 year time period, equivalent to 0.5 Mg CO_2e ha^{-1}. The T_{av} CO_2 stock of *Acacia* plantations is 173.3 Mg CO_2e ha^{-1} (47.4 Mg C ha^{-1}), thus, the net climate benefit of oil palm plantations is 172.8 Mg CO_2e ha^{-1} over a 100 year time period.

6.4.6. Scenario predictions

A 1 Mha piece of land was used to determine the carbon and CO_2e outcomes of different possible FLR scenarios. In T_0 this 1 Mha area stored a total of 69.9 Mt C (Figure 54). Degraded forest, immediately post-logging, stored 68.7 Mt C or 98% of the total carbon, assuming a carbon content of 137.3 Mg ha^{-1} (Table 34), whilst abandoned agricultural land stored just 1.2 Mt C or 2% of total carbon (Figure 54).

Scenario 1 represents a conservation FLR approach, where the entire 1 Mha area was left to naturally regenerate back to an intact forest state. The T_{av} carbon stock was 177 Mt C, over 1 Mha, with a net C change of 107 Mt C (or 392 Mt CO_2), representing a 153% increase in carbon storage (Figure 54). The T_{av} carbon storage in degraded forest recovering back to intact forest, was 99 Mt C (in 0.5 Mha), approximately 20 Mt C more than the T_{av} carbon storage of abandoned agricultural land recovering back to intact forest. However, despite having higher T_{av} carbon storage the net C change in degraded forest was 2.6 times lower than in recovering abandoned agricultural land, at 77 Mt C and 30 Mt C, respectively (Figure 54). These difference in net C change and time-averaged carbon result from differences in T_0 carbon stocks. Abandoned agricultural land has a low

T_0 carbon stock, meaning that the net change in carbon was much greater compared to recovering degraded forest, however, it will take longer for abandoned agricultural areas to reach the high carbon values, therefore time averaged carbon is lower. Rotational logging, oil palm and timber plantation land uses had net C change of between 5.7 Mt C and 6 Mt C (Figure 54)

Scenario 2 represents a possible example of mixed land use FLR. Half of the degraded forest area (0.25 Mha) was retained as forest and left to naturally regenerate, with 0.25 Mha being used for rotational logging. All 0.5 Mha of abandoned agricultural land were used for some form of tree-based agriculture (Agroforestry = 0.25 Mha; oil palm plantation 0.125 Mha; Timber plantations = 0.125 Mha). The T_{av} carbon stock was 118 Mt C over 1 Mha, with a net C change of 47.7 Mt C (168.2 Mt CO_2e); representing a 68%, increase in carbon storage (Figure 54). Recovering degraded forest stored 42% (49.3 Mt C) of T_{av} carbon stock, followed by recovering abandoned agricultural land at 34% (40.3 Mt C). Agroforests, oil palm plantations and timber plantations stored just 12%, 6%, and 5% of T_{av} carbon stocks, respectively (Figure 54). The net C change was also highest in recovering degraded forest (15 Mt C), followed by agroforestry (13.8 Mt C),

Scenario 3 represents an exploitative FLR approach, with the entire 1 Mha area being converted to oil palm plantations. The T_{av} carbon stock was 60.6 Mt C, with a net C change of -9.3 Mt C (or -80.9 Mt CO_2e), representing a 13% decrease in carbon storage (Figure 54). The time average carbon stocks in degraded forest and abandoned agricultural land converted to oil palm plantations is almost identical, at 30.5 Mt C and 30.1 Mt C, respectively. The net C change was -38.2 Mt C in degraded forest converted to oil palm, where as, net C change was 28.9 Mt C in abandoned agricultural land converted to oil palm. This reiterates the importance of selecting appropriate FLR options that take into account the original land use at time of restoration to ensure net positive climate benefits. Large negative emissions of -80.9 Mt CO_2e, includes emissions from N_2O (converted to CO_2e) of 46.8 Mt CO_2e. If these emissions were not accounted for the net CO_2e change would be lower at -34 Mt CO_2e. However, this would still represent a source of CO_2 rather than a sink, as observed in scenario 1 and 2. The negative carbon storage observed in scenario 3 highlights the dangers of using oil palm as an FLR option. Unsurprisingly scenario 1 offers the greatest carbon storage potential, with a T_{av} carbon storage, 51% greater than scenario 2, and 192% greater than scenario 3.

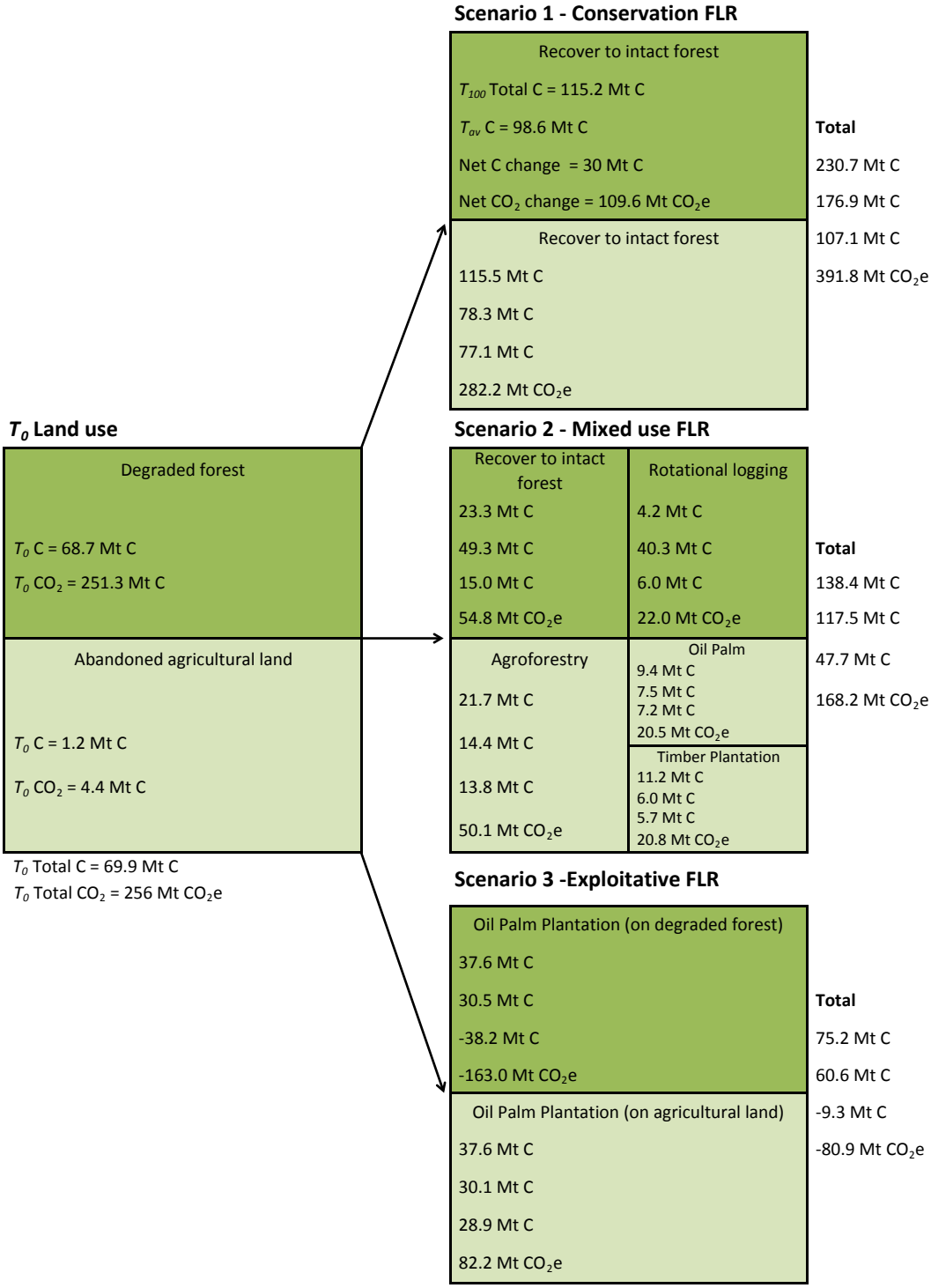

Figure 54. Scenario predictions for a sample 1 Mha of forest. Dark green = degraded forest in T_0, assumed to have a C stock of 137.3 Mg ha^{-1}. light green = abandoned agricultural land at T_0 assumed to have a C stock of 2.4 Mg ha^{-1}. Results in scenario 1 to 3 are ordered as follows: Total carbon storage across area at T_{100}, in Mt C (1 Mt = 1x10^6 Mg), T_{av} carbon storage across area, in Mt C, net change in carbon from T_0 to T_{av}, in Mt C, and change in CO_2e from T_0 to T_{av}, in Mt CO_2e.; calculated as T_{av} CO_2 storage - T_0 CO_2 storage + T_{av} CO_2 emissions (from N_2O). Number within boxes refer to carbon stock for named FLR land use option within set area. Totals refer to total carbon stock across entire 1 Mha

6.5. Discussion

As would be expected, different land use options have highly variable carbon sequestration rates and time averaged carbon stocks (Table 33, Figure 53). All naturally regenerating land use options, which includes; regenerating degraded forest, regenerating abandoned agricultural land and rotationally logged forest, have higher time averaged carbon stocks in comparison to TBA land use options (Figure 53). However, whilst TBA options have lower time averaged carbon stocks than naturally regenerating FLR options they still have much higher carbon storage than traditional agricultural crops, which has been estimated to range between 2 and 15 Mg ha^{-1}, depending on crop (Ziegler et al., 2012).

Thus, on a purely carbon standpoint, naturally regenerating land use options should be favoured as they offer the greatest carbon storage and climate change mitigation potential. Using FLR as a strategy to restore forest over large spatial scales aims to integrate multiple land uses, therefore in some areas other outcomes such as food or timber production are considered alongside carbon storage (Chazdon et al., 2015). Prior to restoration activities taking place the desired outcomes of restoration, which includes carbon storage, biodiversity protection and food production must be determined (Murcia et al., 2015).

It has been shown that large net carbon benefits are possible from forest restoration over large spatial scales (Figure 54). However, carbon outcomes are highly variable depending on the land use options selected for restoration and therefore careful planning is required to ensure a positive carbon balance. The results of this chapter have highlighted four recommendations that policy makers and land managers should take into account when planning landscape scale forest restoration (FLR).

Areas of degraded forest should remain as forest. Degraded forest areas, which in this study refers to naturally regenerating logged forest and rotational logging land uses, have the highest T_{av} carbon stock (Figure 53), higher than any TBA land use. Therefore any areas of degraded forest should be retained as forest and left to naturally regenerate, as this offers the greatest carbon benefit. In addition to carbon sequestration, naturally regenerating

forests also offer biodiversity co-benefits (Berry et al., 2010), soil protection, and watershed protection benefits that are greater than other TBA land uses (Bruijnzeel, 2004).

Natural regeneration of abandoned agricultural land should occur over the largest area possible. Naturally regenerating forests have the third highest T_{av} carbon stock (Figure 53), following degraded forest and rotational logging land uses. Therefore land mangers should be encouraged to allow as large an area as possible to naturally regenerate back to an intact forest. Naturally regenerating forests on abandoned agricultural land have large carbon benefits (see results of chapter 2) alongside proven biodiversity co-benefits (Gilroy et al., 2014). The large areas of forest, naturally regenerating on abandoned agricultural land, have been shown to offer large carbon sequestration potential in a recent study by Chazdon et al. (2016b) from the Neotropics. They found a total of 2.4 Million km^2 of secondary forest (<60 years old), which they estimated could sequester 8.5 Pg C over 40 years of left to naturally regenerate. In additional they estimated that 2 Pg C could be sequestered if 40% of recently abandoned pastures (0.5 Million km^2) were also allowed to regenerate. Demonstrating that in large scale natural benefits would be possible.

Palm oil plantations should not be considered as a restoration option. The large N_2O emissions associated with fertiliser use in palm oil plantations, estimated at 46.8 Mg CO_2e over 100 years, mean that they should not be incorporated into FLR schemes, despite technically meeting the FAO definition of 'forest' (FAO, 2000). In addition palm oil plantations have detrimental effects on biodiversity (Fitzherbert et al., 2008) and soil properties. (Guillaume et al., 2016). Furthermore, this study does not take into account the sources and sinks of carbon emissions from soils. Palm oil plantations are often planted on peat land, which have extremely high carbon storage. A study by Koh et al. (2011), estimated that in the 880,000 ha of oil palm plantations, planted on peat lands in Indonesia and Malaysia, a total of 4.6 million Mg C yr^{-1} would be emitted from peat oxidation, and a further 0.7 million Mg C yr^{-1} of carbon sequestration from peat accumulation would be loss. If these large sources of emissions from peat oxidation were accounted for then it is likely that palm oil plantations are a net source of carbon to the atmosphere and therefore should not be used for landscape restoration.

T_{av} carbon storage values should be used rather than instantaneous carbon storage values and time period used to calculate T_{av} should be long. In this study all estimates of total

carbon storage are based on the assumption that planting occurs on year one (T_1), meaning that instantaneous carbon stocks for a given year (which in this study is T_{100}) are highly dependent on year of planting and the rotation length of a particular TBA land use type. If the given year coincides with the end of a rotation period then total carbon storage is high. For example at T_{100} Eucalyptus plantations have a total carbon stock of 172.9 Mg C ha^{-1} coinciding with the final year of a 20-year rotation length, whereas in rotational logged forest total carbon stock is lower, at 154 Mg C ha^{-1}, coinciding with year ten of a 30-year rotation period. This means that instantaneous carbon stocks are poor for making comparisons between land use types.

Using T_{av} carbon storage allows for comparisons to be made between different land use options, whilst accounting for carbon gains from sequestration and carbon losses from timber harvest over an entire rotation length (Yang et al., 2016), therefore T_{av} carbon stock are not so dependent on the year of planting. Using T_{av} carbon storage also allow for variation in the time of planting (Palm et al., 1999), in a real-world situation all areas would not be planted within a single year and assumed in this study. By using T_{av} carbon storage this effect is averaged out over a longer time period, thus, should not be so problematic (Palm et al., 1999).

However, the minimum time period over which T_{av} carbon storage is calculated should greater than a full rotation length (Palm et al., 1999), and ideally calculated over multiple successive rotations in order to establish a stable T_{av} carbon storage value. Furthermore, in naturally regenerating systems, which continually accumulation carbon until an asymptotic maximum, a long time period is required to calculate T_{av} carbon storage. This gives a true representation of the full carbon storage potential available from naturally regenerating land uses. For example, T_{av} carbon storage of abandoned agricultural land, calculated over a 20 year time period, is just 49.6 Mg C ha^{-1} compared to 156.6 Mg C ha^{-1} when calculated over a 100 year time period (Figure 53). Short time horizons of 20 years have been seen in FLR planning exercises from the WRI (IUCN and WRI, 2014), which present carbon storage in timber plantations of 59.4 Mg C ha^{-1} and in Naturally regenerating forest of 39.5 Mg C ha^{-1}. Using short time horizons to estimate T_{av} carbon storage has important policy implications, as the resulting values present timber plantations as having greater carbon storage potential than naturally regenerating forest. However the results of this study clearly show that naturally regenerating land use options offer much greater carbon benefits than TBA land use options.

6.5.1. Scenario projections

There is a great need for spatially explicit projections of potential carbon sequestration from FLR at a pan-tropical scale to assess the likely contribution that this could make to mitigating climate change. There have been attempts to predict the area of land available for restoration and quantify the carbon sequestration potential following restoration at a regional scale, for example the WIR and IUCN estimate there are 2 billion ha available globally for restoration (Minnemeyer et al., 2011), and the UNEP, estimated that restoring 350 Mha could sequester 1 Pg C yr^{-1} (UNEP, 2015). The three scenarios presented in this chapter assume that in a 1 Mha area, 50% (0.5 Mha) is degraded forest immediately post logging, and 50% is abandoned agricultural land with carbon storage of close to zero at T_0. However in reality T_0 carbon storage would be more variable, with smaller forest stands of different ages and different carbon storage. Furthermore T_0 land use is likely to be more complex, with small fragments of various land uses rather than in one contiguous block (Laurance et al., 1998). However, these scenarios are not intended to be spatially explicit, or representative of current land use at a particular location. Rather, these scenarios are illustrative of the differences in carbon sequestration resulting from different FLR management options.

Scenario 1 and 3 represent the extremes, from a conservation FLR approach (scenario 1) to an exploitative FLR option (scenario 3), and therefore are unlikely in real world situations. Scenario 1, which allows natural regeneration to intact forest over all 1 Mha is particularly unlikely, due to the pressures of converting degraded forest to other more profitable land uses (E.g. Fisher et al., 2011). However, scenario 1 clearly demonstrates the huge carbon storage capacity that is possible in naturally regenerating forest, as seen by Chazdon et al. (2016b).

Scenario 3 may be unlikely under an FLR scheme as it results in large emissions; however, the conversion of large areas of degraded forest to palm oil plantations in Southeast Asia, particularly in Indonesia and Malaysia is not uncommon, with Koh and Wilcove (2008), predicting that 55% to 59% of palm oil expansion came at the expense of primary and logged forest in Malaysia between 1990 and 2005. The large negative net carbon balance, and larger emission when considering N_2O emissions, in scenario 3 offers clear evidence that technically forest cover could be maintained to the land surface, however this would

to add to the climate change mitigation problem rather than address it. For this reason I recommend excluding palm oil plantations from FLR management strategies.

Scenario 2 offers just one of many possible mixed-use FLR options, with different mixed-use FLR options resulting in highly varied carbon storage. In real world situations the final plan for mixed-use FLR will be dictated by current land use, the needs of the local population and the aims of land managers (IUCN and WRI, 2014). However, one thing is clear, to ensure net positive carbon outcomes from FLR, degraded forest land must be retained and either left to naturally regenerate or be used for low intensity rotational selective logging, and should not be converted to a tree based agricultural system that has lower time averaged carbon storage.

6.5.2. Global restoration commitments

Improving our understanding of carbon storage and net climate benefits in FLR systems is timely considering the ambitious targets for forest restoration globally including: the New York Declaration on Forests (UNFCCC, 2014), the BONN Challenge (The BONN Challenge, 2016) and the convention on biological diversity; Aichi biodiversity targets (CBD, 2013). Specifically the New York Declaration on Forest aims to restore 350 Mha of forest by 2030. Across the tropics and sub-tropics to date, 35 countries have committed a total of 248 Mha. These commitments have been made under various schemes including; The BONN Challenge, AFR100 (WRI, 2015a) and Initiative 20X20 (WRI, 2015b). In addition, commitments have been made as intended nationally determined contributions (INDC) following the Paris climate change talks in 2015 or via national programmes not linked to any international schemes.

In 24 countries the area committed to different restoration methods has been made public (The BONN Challenge, 2016) (See Appendix 9 for list of commitment area by country). Plantation forests contribute 45% (± 13.3) of commitments, over 20% more than any other restoration method. Assisted natural regeneration, agroforestry and natural regeneration each constitute 22% (± 11), 21% (± 13), and 11% (± 10), of commitments, respectively (Table 35). To predict a first-order estimate of the total carbon that may be stored later this century across 350 Mha, the proposed area of the New York Declaration on Forests (UNFCCC, 2014), I use the areas allocated to differing restoration land uses as a

guide to estimate the total area under each restoration method, and multiplied by the carbon stocks estimated in this chapter (Table 34).

I estimate that after 100 years, 350 Mha of restored land would store 48 Pg C, with a 100 year time averaged carbon stock of 33.7 Pg C, and after subtracting the initial carbon stored on the land prior to restoration efforts, a net carbon stock change of 22.4 Pg C (Table 35, Figure 55). This is large potential store of carbon within the terrestrial biome, however, using this T_{av} carbon stock, equates to a mean carbon sequestration rate of just 0.37 Pg C yr^{-1} (Carbon sequestration rate = T_{av} carbon storage/100) across the entire 350 Mha restored area over 100 years. This is much lower than the carbon sequestration rates predicted by the UNEP (UNEP, 2015) over a similar area, who estimated that if 350 Mha were restored back to intact forest, then by 2030, restored lands would be sequestering 1.04 Pg C yr^{-1}. Using the carbon sequestration rates estimated in this study I predict that if all 350 Mha were restored back to intact forest, there would be a T_{av} carbon stock of 58 Pg C, with a sequestration rate of 0.6 Pg C yr^{-1}, lower than estimated by the UNEP. Another report by Wolosin (2014) predicted total carbon sequestration over 350 Mha between 2011 and 2030, assuming a linear increase in the area of land under restoration management from 2011 to 2030. They predicted that restored lands would be sequestering between 0.6 and 0.9 Pg C yr^{-1} by 2030, which is similar to my estimate if all 350 Mha were to be restored back to intact forest. However, it is highly unlikely that all 350 Mha of land committed under the NYFD would be restored back to an intact forest state, indeed, 45% of the land area already committed, is to be planted with timber plantations (Table 35, Appendix 9), meaning that these prediction is massively overestimating the carbon sequestration potential of restoration.

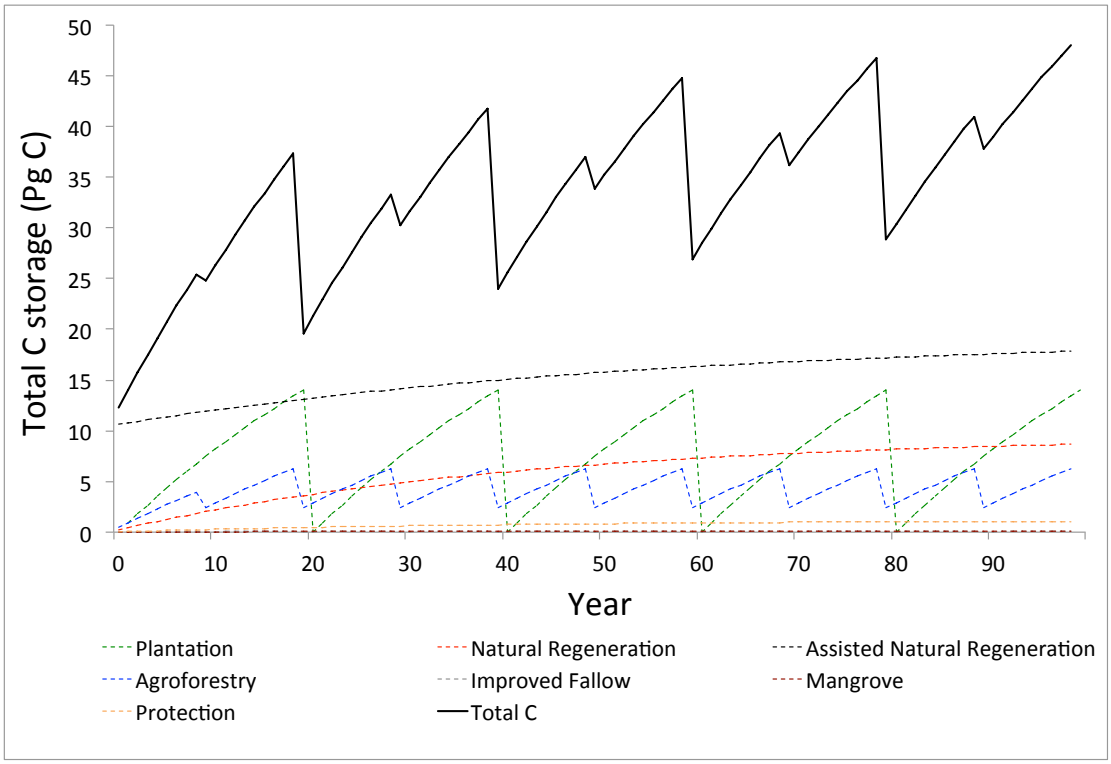

Figure 55. Total carbon storage for 350 Mha restoration commitments, over 100 years. Solid line shows total carbon storage, dashed lines show total carbon storage for each land use type proposed under the NYDF by Wolosin (2014).

Despite a relatively low total carbon sequestration rate of 0.36 Pg C yr^{-1}, over a 350 Mha area, such removals of carbon from the atmosphere could still offer climate benefits. This total carbon sequestration rate is greater than the predicted tropical forest annual carbon flux of 0.16 Pg C yr^{-1} (Grace et al., 2014). Additionally, Grace et al. (2014), estimated a tropical carbon sink of 1.85 Pg C yr^{-1} and a tropical carbon source of 2.01 Pg C yr^{-1}, with 1.2 Pg C yr^{-1} coming from deforestation and forest degradation. If 350 Mha of forest were to be restored and forest loss were halted by 2030, as stated in the NYDF (UNFCCC, 2014) then the resulting tropical forest carbon sink would be 1.56 Pg C yr^{-1}, an important contribution to offsetting carbon emissions and mitigating climate change. Fossil fuel emissions are currently estimated to by 9 Pg C yr^{-1} with 1 Pg C yr^{-1} from land use change globally (Le Quéré et al., 2015), therefore going from a source of 1 Pg C yr-1 from land use change to a sink of 1.56 Pg C yr^{-1}, would result in a large total reduction of 2.56 Pg C yr^{-1}, which would contribute hugely to climate change mitigation, and could help in the transition away from fossil fuel use (Houghton et al., 2015)

Over 350 Mha, plantations, which cover 45% of the total restored area, store just 22% of the time averaged carbon stock, whereas assisted natural regeneration, which covers 22% of total restored area, stores 45% of time average carbon stock (Table 35). The lower time average carbon stock in plantations reiterates the results of this chapter, which show that naturally regenerating land use FLR options offer greater carbon storage potential than TBA land use options (Table 34). Furthermore, the differences in carbon storage suggests that countries who have yet to determine restoration methods, should be encouraged to use naturally regenerating land use options over as large an area as possible, to attain the highest possible carbon storage, and increase the possible carbon sink from forest restoration.

6.6. Conclusions

Landscape scale restoration has the ability to sequester large quantities of carbon from the atmosphere. However, careful selection of restoration land use options is required to ensure a net positive carbon balance. Naturally regenerating land use options offer much greater carbon storage potential compared to TBA land use options. Lower carbon value TBA land uses present a compromise between higher carbon value naturally regenerating forest and other benefits such as food and timber production. However, the results of this chapter strongly suggest that degraded forest should remain as forests to ensure net positive carbon balance and advise against allowing oil palm plantations to be incorporated into landscape scale restoration plans due to the large N_2O emissions resulting from fertiliser application.

The higher 100 year time average carbon stocks of naturally regenerating land use options clearly show that naturally regenerating forest must be included in in landscape scale restoration plans to ensure a large net positive carbon balance. With a number of tropical countries yet to decide how to restore their committed land areas, and few having begun the process of large scale restoration, now is the time advise tropical forest nations and the international community that to meet ambitious climate targets large areas will be required to be committed to regeneration back to natural forest, as this offers the greatest carbon sequestration potential and therefore the greatest climate change mitigation potential.

Table 35. Total carbon storage in 350 Mha restoration area. Showing percentage of area per restoration method, total area restored using each method, carbon stocks at T_0, T_{100} and T_{av} (Mg ha^{-1}), Pg C at T_0, T_{100} and T_{av} and Net C change (Pg C) from T_0 to T_{av}. Values for T_0, T_{100} and T_{av} (Mg ha^{-1}), taken from Table 34 as; a = plantation (mean of Eucalyptus and Acacia), b = abandoned agriculture, c = degraded forest, d = agroforestry, e = Protection areas include restoration to control erosion or protect watersheds.

			Mg ha			Pg (total over 350 Mha)			
Restoration Method	% Of area	Total Area (Mha)	T_0 C (Mg ha^{-1})	T_{100} C (Mg ha^{-1})	T_{av} C (Mg ha^{-1})	T_0 C (Pg)	T_{100} C (Pg)	T_{av} C (Pg)	Net C change (Pg)
Plantation [a]	44.8	157	2.4	89.2	48.1	0.4	14.0	7.5	7.2
Natural Regeneration [b]	10.7	37	2.4	230.9	156.6	0.1	8.7	5.9	5.8
Assisted natural regeneration [c]	22.1	77	137.3	230.4	197.2	10.6	17.8	15.3	4.6
Agroforestry [d]	20.7	72	2.4	86.8	57.4	0.2	6.3	4.2	4.0
Improved Fallow [d]	0.2	1	2.4	86.8	57.4	0.002	0.1	0.05	0.04
Mangrove [b]	0.1	0	2.4	230.9	156.6	0.001	0.1	0.1	0.1
Protection [b,e]	1.3	5	2.4	230.9	156.6	0.011	1.1	0.7	0.7
Total	100	350			Total (Pg C)	11.3	48.0	33.7	22.4

7. Conclusions

7.1. Main findings

Restoration of tropical forest is widely assumed to be an effective climate change mitigation strategy, whilst also offering biodiversity co-benefits (Chazdon, 2008, Crouzeilles et al., 2016, Houghton et al., 2015). However, knowledge of how naturally regenerating forests recover following disturbance, how active restoration effects forest recovery, and the associated uptake of carbon and biodiversity from restoration, remains poorly quantified. Improving understanding of forest recovery, both as a result of natural regeneration and active restoration, is needed to assess the climate change mitigation potential of landscape scale restoration. This thesis aimed to 1) quantify the rate of recovery in naturally regenerating forest following different types of disturbance, 2) quantify the rate of recovery in actively restored forests, and 3) project expected amounts of carbon storage and climate mitigation from landscape scale restoration.

7.1.1. Impacts of land use type on rate of recovery in naturally regeneration forests (Objective 1; Chapter 2)

This thesis presented data on the recovery of aboveground biomass (AGB) in naturally regenerating forests following four different tropical land uses: pasture, permanent agriculture, shifting cultivation and selective logging, from 71 sites and 68 studies. To my knowledge this is the largest analysis of forest recovery literature from the tropics, using twice as many studies as past efforts assessing the recovery of AGB in forests recovering on abandoned agricultural lands (Poorter et al., 2016, Bonner et al., 2013). I found that AGB accumulation in naturally regenerating forest was rapid, with a rate of 4.9 Mg dry mass ha^{-1} yr^{-1} in the first 20 years of recovery, slowing to 4.3 Mg ha^{-1} yr^{-1} when the full time period (0 – 40 years) was considered. No effects of land use type (pasture, agriculture, and shifting cultivation), on AGB accumulation were observed, suggesting that the type of disturbance experienced was not an important factor in determining recovery rates.

However, there was a positive relationship between mean annual temperature and AGB accumulation, with increased rainfall leading to higher AGB accumulation rates.

Future research directions

Whilst the results of this thesis show that there was no effect of land use type or continent on AGB accumulation, estimated AGB accumulation rates exhibit large variation. It is likely that differences in conditions at the site level explain some of the variation in recovery rates, however, other biotic and abiotic factors such as soil fertility, soil structure, duration of land use and the surrounding vegetation matrix could also potentially influence recovery. Further investigation into different factors that could affect the rate of AGB accumulation would help to reduce the variation in estimates, and provide a clearer understanding of what factors influence natural regeneration.

This study also highlighted the paucity of data from Africa, with analysis including just three studies from the region, including the data presented in chapter 3 of this thesis (Appendix 10, Wheeler et al., 2016). There is a clear need for more research regarding AGB recovery in disturbed areas to be conducted across Africa. Furthermore, with an estimated 191 million ha of regrowth forest in Africa (Pan et al., 2011), improved understanding of how rapidly these large areas of regrowth forest are sequestering carbon could have large impacts on the tropical forest carbon balance.

Findings from this study also point out how few studies use repeat measurements of permanent sample plots (PSP) to monitor AGB recovery. Just 22% of studies included in analysed used PSPs to assess changes in naturally regenerating forest, compared to 78% of studies, which used chronosequence methods. The use of PSP networks, which can be used to monitor long-term changes in AGB, woody productivity, recruitment and mortality (e.g. Lewis et al., 2013, Lewis et al., 2009, Brienen et al., 2015) is common practice in old-growth tropical forests (e.g. the Rainfor, AfriTRON and CTFS forest plot networks), as repeat sampling offers far greater accuracy in estimated of carbon stock changes through time, in comparison to chronosequence methods. Similar networks of forest plots in naturally regenerating forest, would be invaluable to monitor long-term changes in carbon storage and forest function at a regional scale,

7.1.2. Effects of active forest restoration on AGB and biodiversity (Objective 2; Chapter 3 and Chapter 4)

Fieldwork at two sites, in Uganda and Malaysian Borneo, both showed that active tropical forest restoration increased the rates of AGB accumulation, recovery of forest structure and increased tree diversity compared to areas that were not actively restored. However the magnitude of these effects is dependent on the type of land use when restoration management interventions take place. In Kibale national park, Uganda, land had been cleared of original forest cover and used for subsistence agriculture. When areas were abandoned the resulting land was heavily degraded and regularly burnt. Restoration using a combination of fire protection and tree planting led to increases in AGB and tree diversity over 18 years, with an AGB accumulation rate of 3.9 Mg ha^{-1} yr^{-1}. 18 years after restoration took place 70% of the AGB was found in planted stems, which demonstrates the importance of the restoration treatment for AGB and therefore carbon. After 18 years, tree species were also dominated by planted species (63% of stems), which suggested that species richness and species composition to reach primary forest levels, will require a much longer duration of time.

Whilst AGB and tree diversity in Kibale Nation Park were still significantly lower than seen in primary forest, this was not the case in the restoration project in Sabah, Borneo. The project area was selectively logged in 1989 and part of it restored in 1999, using a combination of enrichment planting and climber cutting. In logged areas that had received the restoration treatment, AGB and tree (≥10 cm DBH) species richness, were the same as observed in primary forest, on average, 15 years after restoration had taken place. Whereas, in logged areas that had not been restored, AGB and species richness were significantly lower than in primary forest. Additionally, AGB accumulation was more than twice as fast in restoration areas compared to logged areas, at 7.8 Mg dry mass ha^{-1} yr^{-1} and 3.5 Mg ha^{-1} yr^{-1}, respectively. Significant differences in AGB accumulation and tree diversity were also related to the intensity of logging, with heavily logged areas having lower AGB and species richness and lightly logged areas. However, despite high species richness being observed in restoration areas, species composition was still markedly different compared to primary forest, as was the case in Kibale. This is the first study to compare, AGB, forest structure and biodiversity, in selectively logged forest and selectively

logged forest that has undergone restoration, meaning that it offers new insights into the possible carbon and biodiversity benefits of active restoration within logged areas.

In both the Ugandan and Malaysian studies recovery of AGB and biodiversity as a result of restoration interventions was observed, however, recovery was more rapid in the Malaysian study on selectively logged forest, with forest structure and species richness similar to primary forest within 15 years of restoration in some areas. The similarity of forest structure and species richness to primary forest after 15 years of restoration in the Malaysian study is partially due to the standing vegetation present in the Malaysian study at the time of restoration; meaning that forest structure and tree diversity were more similar to primary forest at the time of restoration in comparison to Kibale, where the original vegetation was very low AGB and low diversity grasses.

The biggest limitation in both of these studies is the lack of baseline data collected at the time of restoration. In Kibale this problem was overcome by establishing plots in grassland areas that had been abandoned but had not yet received the restoration treatment. These grassland plots had undergone the same annual burning regime as the plots measured in restoration areas, and therefore they were considered to be representative of the plots prior to restoration.

The Malaysian project had differing limitations. The first census data were collected in 2007, approximately eight years after restoration was conducted, and 18 years after logging, thus the AGB after logging and exactly what was removed was not known precisely, and the AGB and species diversity of areas at the time of restoration is not known. Furthermore, selective logging is highly heterogeneous, with some areas heavily impacted by logging activities such as skid trails and log landings and other areas relatively untouched (Whitmore, 1984), resulting in highly variable AGB following logging. To try and account for some of this variation, plots were first classified as having undergone high, mid or low intensity logging, based on a number of criteria. This was done to ensure an even distribution of plots from each class, in both the logged and the restoration areas. Classifying plots in this way, approximately 26 years after logging took place, has limitations as plots may have recovered considerably since logging took place, however, by adhering to criteria (table x), I believe these classifications to be reasonable approximations of initial logging intensity. To determine whether differences in forest recovery, observed between logged and restoration plots were actually due to restoration

management and not due to other confounding factors, the following hypothesis were tested: *H1 - Forest were different prior to logging*, *H2 – Forests allocated to restoration were logged differently* and *H3 – Forest were different prior to restoration,* using available data. Soil and logging data showed that restoration plots had slightly lower soil fertility and were logged more heavily; despite this restoration areas were recovering AGB more rapidly. From this I concluded that the observed differences between logged and restoration areas were due to restoration treatment, and not due to systematic differences between logged and restoration plots.

However, if baseline data were available, plots in restoration and logged areas with similar forest structure, in terms of AGB, BA, WD and stem density, at the time of restoration (1999/2000) could be selected and recovery through time could be compared, giving much more accurate results. These studies therefore highlight the necessity of collecting baseline data, regarding, AGB, forest structure and biodiversity, at the time of restoration, to enable accurate monitoring of changes in forest structure and biodiversity through time.

Future research directions

In Kibale, one the biggest problems identified in restoration areas was the spread of the invasive shrub *Lantana camara*. *L. camara* was the most common shrub in restoration plots and in some areas it was becoming very dominant. Further research is required to evaluate the spread of *L. camara* in the restoration area and monitor its effects of tree growth and mortality. Additionally, research into the effectiveness of methods to control the spread of *L. camara*, in needed, and could help inform management decision within Kibale.

In the Malaysian project, very few planted stems were identified in the plots monitored. This suggests that other management interventions, which include, climber cutting of vines and bamboos and liberation cutting of naturally regenerating seedlings, are having the biggest impact on recovery in restoration areas. Climber cutting as a management intervention has been shown to help accelerate AGB recovery in parts of the Amazon (César et al., 2016), and evidence from Chapter 4 would suggest that this is also the case in Southeast Asia, however, more detailed investigation into the impacts of climber cutting

on forest recovery within restoration forest is needed. Such research could help aid management decisions in restoration projects.

Conducting research in these two restoration projects, which have employed different restoration management and monitoring strategies, has identified a number of practices that should ideally be adopted in restoration projects to enable successful monitoring:

1) Restoration projects should include control sites that have not undergone the restoration treatment, so the effect of restoration on forest recovery can be compared to a 'business as usual' scenario.
2) Randomisation of restoration and control areas should be conducted to ensure that control sites are not just placed in areas that are already naturally regenerating more rapidly.
3) If more than one management intervention is being employed then ideally fully factorial experiments should be established to identify which interventions have the greatest impact on recovery. For example, in the Malaysian site, a randomised block design with plots in selectively logged areas assigned to one of the following treatments; 1) control (no treatment), 2) climber cutting, 3) enrichment planting or 4) climber cutting + enrichment planting, would allow the analysis of the different management interventions to be assessed.
4) Forest plots should be established and monitored prior to restoration management taking place, so the original site conditions are known
5) Forest plots should be re-censused at regular intervals so changes in AGB, forest structure, and diversity can be assessed.
6) Records of what species were planted and where should be kept, so assessments of planted seeding survival can be done.
7) Small stem size classes (<10 cm DBH) should be monitored, as in young planted forest small stem may contribute a large proportion to AGB. Furthermore, monitoring of small stems also gives information about the diversity of species newly recruited seedlings.
8) Records of whether stems were planted or non-planted should be kept to assess the importance of planting on forest structure and diversity.
9) All monitoring data should be carefully stored electronically, so it is available for subsequent censuses.

Adopting such protocols in restoration projects would allow for accurate monitoring, allowing for the impacts of restoration on AGB, forest structure and biodiversity to be assessed, which is clearly needed.

7.1.3. Carbon storage potential of landscape scale restoration (Objective 3; Chapter 5)

The results of this thesis clearly show that, of the six different land use options available for landscape scale restoration, naturally regenerating options had the highest time averaged carbon storage. Naturally regenerating options included, degraded forest recovering following selective logging, rotation selective logging and abandoned agricultural land. Whilst, tree based agricultural options including: timber plantations, agroforestry and oil palm plantations, had much lower time averaged carbon storage. These differences in time averaged carbon storage result in large difference in potential carbon storage when scaled up across the landscape. In a hypothetical one million ha restoration area, which has an initial land cover of half degraded forest and half abandoned agricultural land, I predict that restoring all one million ha to a natural forest state would give a time averaged carbon stock of 177 Mt C, and a net carbon balance of 107 Mt C (392 Mt CO_2e). However, in most areas of the world widespread landscape restoration of forest, utilising complete restoration back to natural forest over the entire landscape is unlikely. A more likely scenario it that, multiple land use types will be integrated within the landscape offering carbon sequestration benefits alongside other benefits such as timber and crop production. If a mixed use restoration option were undertaken, retaining the degraded forest area (0.5 million ha) as forest, and using some of this area for selective logging for income (0.25 million ha) and the rest left to recover (0.25 million ha), and then converting the abandoned agricultural areas (0.5 million ha) to tree based agricultural land uses, across the range of possibilities (0.25 million ha agroforestry, 0.125 million ha each of timber plantations and oil palm) then time averaged a carbon would be 118 Mt C with a net carbon balance of 48 Mt C (168 Mt CO_2e), half the amount that would have been sequestered had all 1 million ha been restored to forest.

Finally if all one million ha were converted to oil palm plantations, which under certain definitions can be classified as forest, an exploitative form of landscape scale restoration, then time average carbon storage would be 61 Mt C, however the net carbon balance

would be -9 Mt C, due to conversion of the original land cover from degraded forest to plantations. Furthermore including N_2O emissions from fertiliser application produced a large negative net climate balance of -81 Mt CO_2e from oil palm plantations. These findings firstly indicate that the natural regeneration of forests offers by far the largest carbon benefits. Secondly, they indicate that landscapes can have a net positive carbon balance via a combination of naturally regenerating forest and selective logging alongside some tree based agricultural land uses, on abandoned agricultural land. However, carbon benefits are more modest. Finally, a cynical approach of classifying palm oil plantations as forest restoration, and converting areas to only this land cover type can be a net contribution to climate change rather than mitigation. Large-scale palm oil or similar intensive tree-based agriculture should be excluded from landscape scale restoration plans if climate change mitigation is one of the considerations.

Future research directions

Predicting carbon storage under different restoration scenarios over a one million ha area illustrates the possible scale of carbon storage over a large spatial scale. However, the scenarios presented in my thesis were to examine the extreme scenarios (all restoration to natural forest, all palm oil) and do not represent an accurate picture of restoration on the ground. Furthermore, much larger areas of approximately 350 million ha, have been committed for restoration in the tropics (UNFCCC, 2014). This thesis presents a first-order estimated for carbon sequestration over a 350 million ha area, predicting a time averaged carbon stock of 34 Pg C over 100 years, with a mean sequestration rate of 0.36 Pg C. Further research is needed to predict more accurate time average carbon storage and carbon sequestration rates over such large spatial scale, to understand the full impact of forest restoration as a climate change mitigation option.

Additionally, to assess the carbon stocks of large areas of land, relying on plots is not possible. Plots should be used to calibrate remotely sensed data; either airborne LiDAR , or spaceborne optical or radar sensors to scale to the landscape (Mitchard et al., 2012, Asner et al., 2010, Marvin and Asner, 2016, Asner and Mascaro, 2014, Avitabile et al., 2016). This would firstly allow for more precise estimates of the initial carbon stocks of the landscape prior to restoration, and second, progress could be monitored, particularly in the naturally regenerating areas. For land cover types that have harvests of products, care would still

need to be taken that carbon stocks will fluctuate, with large declines after harvest of timber and other products, such fluctuations need to be taken into account when assessing the climate relevant carbon stock changes (perhaps by using time-averaged stocks, as suggested in this thesis).

7.2. Research Implications

The increasing focus of forest restoration as a climate change mitigation strategy means that the findings of this thesis are timely, and have implications for restoration planning and policy. This thesis has clearly shown the importance of naturally regenerating forest for carbon sequestration in two ways. Firstly, that carbon uptake on the land surface is large, per unit area, if forest is managed to allow natural regeneration. The carbon sequestration rates of 4.9 Mg ha^{-1} yr^{-1} (in the first 20 years of recovery), estimated in this study, are in agreement with two other studies assessing carbon sequestration in naturally regenerating forest (Poorter et al., 2016, Bonner et al., 2013). However, results of this thesis also showed that MAP has a significant effect on recovery, which suggests that carbon sequestration would be higher in wetter parts of the tropics. This has important implications in the face of changing climate in tropical regions. Research suggest that the frequencies of drought may increase over coming decades (Cai et al., 2014, Malhi et al., 2008), and therefore if decreases in rainfall could have a negative effect on the carbon sequestration rate, this could possibly reduce the sink potential of naturally regenerating forest.

Secondly, I have shown the importance of incorporating naturally regenerating forest into landscape scale restoration plans, as they offer the greatest carbon storage benefits. This concurs with recent research, which suggests that naturally regenerating forest have a large potential carbon sink of 8.5 Pg C, over 40 years in the Neotropics alone (Chazdon et al., 2016b). My findings present a clear case for retaining degraded forest areas as forest, allowing them to naturally regenerate, as other restoration land use options, such as tree based agriculture, would lead to reductions if carbon storage. Alongside this, increasing tree-based agriculture in low carbon density abandoned agricultural lands could also offer carbon benefits coupled with other benefits such a timber and crop production. These findings have important implications for restoration planning at a landscape scale, and

pose important point for consideration by land managers and policy makers, to ensure that restoration plans offer the greatest carbon sequestration potential. Having clearer understanding of the carbon benefits of different restoration land use options is essential at this time as there are currently close to 250 million ha of lands committed to restoration in the tropics (The BONN Challenge, 2016), which is likely to increase to meet the 350 million ha target of the NYDF (UNFCCC, 2014). Therefore, my findings may help promote the case for naturally regenerating forest to be incorporated into restoration management plans.

I also show that active forest restoration has the potential to help overcome the problems of arrested succession in heavily degraded lands, and help accelerate the rate of forest recovery in degraded forest. I provide new data in the sequestration and biodiversity change in Kibale National Park, Uganda, and in Malaysian Borneo. Furthermore, results presented in thesis are now some of the longest-running experiments estimating carbon sequestration and biodiversity change within actively restoration tropical forests, using permanent repeat sample methods. Therefore these finding improve our understanding of recovery within actively restored forest, and emphasis the benefits of active forest restoration treatments.

7.3. Summary

My findings demonstrate the high rates of carbon sequestration possible within naturally regenerating forests, however, it is possible to enhance rates of recovery via active forest restoration, which also has additional biodiversity benefits. If restoration is conducted over large spatial scales then it could provide an opportunity to sequester large quantities of CO_2 from the atmosphere. As there is an immediate need to mitigate climate change, particularly given that current nationally determined contributions submitted at the Paris climate change talks are estimated to lead to warming of between 2.6˚C and 3.1˚C (Rogelj et al., 2016), then tropical forest restoration could help in the transition (Houghton et al., 2015) to warming of between 1.5˚C and 2˚C.

References

ACHARD, F., BEUCHLE, R., MAYAUX, P., STIBIG, H.-J., BODART, C., BRINK, A., CARBONI, S., DESCLÉE, B., DONNAY, F., EVA, H. D., LUPI, A., RAŠI, R., SELIGER, R. & SIMONETTI, D. 2014. Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biology,* 20**,** 2540-2554.

ACHARD, F., EVA, H. D., MAYAUX, P., STIBIG, H. J. & BELWARD, A. 2004. Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s. *Global Biogeochemical Cycles,* 18.

ACHARD, F., EVA, H. D., STIBIG, H.-J., MAYAUX, P., GALLEGO, J., RICHARDS, T. & MALINGREAU, J.-P. 2002. Determination of deforestation rates of the world's humid tropical forests. *Science,* 297**,** 999-1002.

AFRITRON. 2009. *African Tropical Rainforest Observation Network* http://www.afritron.org/ [Online]. [accessed September 2015].

AIDE, T. M., ZIMMERMAN, J. K., HERRERA, L., ROSARIO, M. & SERRANO, M. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *Forest Ecology and Management,* 77**,** 77-86.

AIDE, T. M., ZIMMERMAN, J. K., PASCARELLA, J. B., RIVERA, L. & MARCANO-VEGA, H. 2000. Forest Regeneration in a Chronosequence of Tropical Abandoned Pastures: Implications for Restoration Ecology. *Restoration Ecology,* 8**,** 328-338.

ALBRECHT, A. & KANDJI, S. T. 2003. Carbon sequestration in tropical agroforestry systems. *Agriculture, Ecosystems & Environment,* 99**,** 15-27.

ALLEN, M. F., ALLEN, E. B. & GÓMEZ‐POMPA, A. 2005. Effects of mycorrhizae and nontarget organisms on restoration of a seasonal tropical forest in Quintana Roo, Mexico: factors limiting tree establishment. *Restoration Ecology,* 13**,** 325-333.

ALVES, D. S., SOARES, J. V., AMARAL, S., MELLO, E. M. K., ALMEIDA, S. A. S., DASILVA, O. F. & SILVEIRA, A. M. 1997. Biomass of primary and secondary vegetation in Rondonia, Western Brazilian Amazon. *Global Change Biology,* 3**,** 451-461.

ANGELSEN, A. 2008. Moving ahead with REDD: Issues, options and implications. Bogor, Indonesia: Centre for International Forestry Research.

ANGELSEN, A., BROCKHAUS, M., KANNINEN, M., SILLS, E., SUNDERLIN, W. D. AND WERTZ-KANOUNNIKOFF, S. 2009. Realising REDD+ : National strategy and policy options. Bogor, Indonesia: Center for International Forestry Research.

ANSELL, F. A., EDWARDS, D. P. & HAMER, K. C. 2011. Rehabilitation of Logged Rain Forests: Avifaunal Composition, Habitat Structure, and Implications for Biodiversity-Friendly REDD+. *Biotropica,* 43**,** 504-511.

APPANAH, S. 1993. Mass flowering of dipterocarp forests in the aseasonal tropics. *Journal of Biosciences,* 18**,** 457-474.

ARONSON, J. & ALEXANDER, S. 2013. Ecosystem restoration is now a global priority: time to roll up our sleeves. *Restoration Ecology,* 21**,** 293-296.

ARORA, V. K. & MONTENEGRO, A. 2011. Small temperature benefits provided by realistic afforestation efforts. *Nature Geoscience,* 4**,** 514-518.

ASHTON, M. S., MENDELSOHN, R., SINGHAKUMARA, B., GUNATILLEKE, C., GUNATILLEKE, I. & EVANS, A. 2001. A financial analysis of rain forest silviculture in southwestern Sri Lanka. *Forest Ecology and Management,* 154**,** 431-441.

ASNER, G. P. & MASCARO, J. 2014. Mapping tropical forest carbon: Calibrating plot estimates to a simple LiDAR metric. *Remote Sensing of Environment,* 140**,** 614-624.

ASNER, G. P., POWELL, G. V. N., MASCARO, J., KNAPP, D. E., CLARK, J. K., JACOBSON, J., KENNEDY-BOWDOIN, T., BALAJI, A., PAEZ-ACOSTA, G., VICTORIA, E., SECADA, L., VALQUI, M. & HUGHES, R. F. 2010. High-resolution forest carbon stocks and emissions in the Amazon. *Proceedings of the National Academy of Sciences,* 107**,** 16738-16742.

ATMADJA, S. & VERCHOT, L. 2012. A review of the state of research, policies and strategies in addressing leakage from reducing emissions from deforestation and forest degradation (REDD+). *Mitigation and Adaptation Strategies for Global Change,* 17**,** 311-336.

AVITABILE, V., HEROLD, M., HEUVELINK, G., LEWIS, S. L., PHILLIPS, O. L., ASNER, G. P., ARMSTON, J., ASHTON, P. S., BANIN, L. & BAYOL, N. 2016. An integrated pan‐tropical biomass map using multiple reference datasets. *Global change biology*.

BACCINI, A., GOETZ, S., WALKER, W., LAPORTE, N., SUN, M., SULLA-MENASHE, D., HACKLER, J., BECK, P., DUBAYAH, R. & FRIEDL, M. 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate Change,* 2**,** 182-185.

BAKER, T. R., PHILLIPS, O. L., MALHI, Y., ALMEIDA, S., ARROYO, L., DI FIORE, A., ERWIN, T., HIGUCHI, N., KILLEEN, T. J., LAURANCE, S. G., LAURANCE, W. F., LEWIS, S. L., MONTEAGUDO, A., NEILL, D. A., VARGAS, P. N., PITMAN, N. C. A., SILVA, J. N. M. & MARTINEZ, R. V. 2004a. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 359**,** 353-365.

BAKER, T. R., PHILLIPS, O. L., MALHI, Y., ALMEIDA, S., ARROYO, L., DI FIORE, A., ERWIN, T., KILLEEN, T. J., LAURANCE, S. G., LAURANCE, W. F., LEWIS, S. L., LLOYD, J., MONTEAGUDO, A., NEILL, D. A., PATINO, S., PITMAN, N. C. A., SILVA, J. N. M. & MARTINEZ, R. V. 2004b. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology,* 10**,** 545-562.

BAKKER, J. P., OLFF, H., WILLEMS, J. H. & ZOBEL, M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science,* 7**,** 147-155.

BANIN, L. 2010. *Cross-continental comparisons of tropical forest structure and function.* Doctor of Philosophy Thesis, University of Leeds.

BANIN, L., FELDPAUSCH, T. R., PHILLIPS, O. L., BAKER, T. R., LLOYD, J., AFFUM-BAFFOE, K., ARETS, E., BERRY, N. J., BRADFORD, M., BRIENEN, R. J. W., DAVIES, S., DRESCHER, M., HIGUCHI, N., HILBERT, D. W., HLADIK, A., IIDA, Y., ABU SALIM, K., KASSIM, A. R., KING, D. A., LOPEZ-GONZALEZ, G., METCALFE, D., NILUS, R., PEH, K. S. H., REITSMA, J. M., SONKE, B., TAEDOUMG, H., TAN, S., WHITE, L., WOLL, H. & LEWIS, S. L. 2012. What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography,* 21**,** 1179-1190.

BARAJAS-GUZMÁN, M. G. & BARRADAS, V. L. 2011. Microclimate and sapling survival under organic and polyethylene mulch in a tropical dry deciduous forest. *Boletín de la Sociedad Botánica de México,* 88**,** 27-34.

BARANGA, J. 1991. *Kibale Forest Game Corridor: man or wildlife?,* Australia, Surrey Beatty & Sons.

BARBOSA, K. C. & PIZO, M. A. 2006. Seed rain and seed limitation in a planted gallery forest in Brazil. *Restoration Ecology,* 14**,** 504-515.

BARLOW, J., GARDNER, T. A., ARAUJO, I. S., ÁVILA-PIRES, T. C., BONALDO, A. B., COSTA, J. E., ESPOSITO, M. C., FERREIRA, L. V., HAWES, J. & HERNANDEZ, M. I. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences,* 104**,** 18555-18560.

BARTOŃ, K. 2015. MuMin: Multi-model Inference. 1.15.6 ed.

BECKNELL, J. M., KUCEK, L. K. & POWERS, J. S. 2012. Aboveground biomass in mature and secondary seasonally dry tropical forests: A literature review and global synthesis. *Forest Ecology and Management,* 276**,** 88-95.

BEER, C., REICHSTEIN, M., TOMELLERI, E., CIAIS, P., JUNG, M., CARVALHAIS, N., RODENBECK, C., ARAIN, M. A., BALDOCCHI, D., BONAN, G. B., BONDEAU, A., CESCATTI, A., LASSLOP, G., LINDROTH, A., LOMAS, M., LUYSSAERT, S., MARGOLIS, H., OLESON, K. W., ROUPSARD, O., VEENENDAAL, E., VIOVY, N., WILLIAMS, C., WOODWARD, F. I. & PAPALE, D. 2010. Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate. *Science,* 329**,** 834-838.

BEKESSY, S. A. & WINTLE, B. A. 2008. Using carbon investment to grow the biodiversity bank. *Conservation Biology,* 22**,** 510-513.

BELLASSEN, V. & LUYSSAERT, S. 2014. Managing forests in uncertain times. *Nature,* 506**,** 153-155.

BENAYAS, J. R., MARTINS, A., NICOLAU, J. M. & SCHULZ, J. J. 2007. Abandonment of agricultural land: an overview of drivers and consequences. *CAB reviews: perspectives in agriculture, veterinary science, nutrition and natural resources,* 2**,** 1-14.

BENEDICK, S., WHITE, T. A., SEARLE, J. B., HAMER, K. C., MUSTAFFA, N., KHEN, C. V., MOHAMED, M., SCHILTHUIZEN, M. & HILL, J. K. 2007. Impacts of habitat fragmentation on genetic diversity in a tropical forest butterfly on Borneo. *Journal of Tropical Ecology,* 23**,** 623-634.

BERRY, N. J., PHILLIPS, O. L., LEWIS, S. L., HILL, J. K., EDWARDS, D. P., TAWATAO, N. B., AHMAD, N., MAGINTAN, D., KHEN, C. V., MARYATI, M., ONG, R. C. & HAMER, K. C. 2010. The high value of logged tropical forests: lessons from northern Borneo. *Biodiversity and Conservation,* 19**,** 985-997.

BETTS, R. A. 2000. Offset of the potential carbon sink from boreal forestation by decreases in surface albedo. *Nature,* 408**,** 187-190.

BHAGWAT, S. A., WILLIS, K. J., BIRKS, H. J. B. & WHITTAKER, R. J. 2008. Agroforestry: a refuge for tropical biodiversity? *Trends in Ecology & Evolution,* 23**,** 261-267.

BIRDSEY, R., PAN, Y. D. & HOUGHTON, R. 2013. Sustainable landscapes in a world of change: tropical forests, land use and implementation of REDD plus : Part I Foreword. *Carbon Management,* 4**,** 465-468.

BISCHOFF, W., NEWBERY, D. M., LINGENFELDER, M., SCHNAECKEL, R., PETOL, G. H., MADANI, L. & RIDSDALE, C. E. 2005. Secondary succession and dipterocarp recruitment in Bornean rain forest after logging. *Forest Ecology and Management,* 218**,** 174-192.

BOLKER, B. M., BROOKS, M. E., CLARK, C. J., GEANGE, S. W., POULSEN, J. R., STEVENS, M. H. H. & WHITE, J.-S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution,* 24**,** 127-135.

BONAN, G. B. 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. *Science,* 320**,** 1444-1449.

BONGERS, F., POORTER, L., HAWTHORNE, W. D. & SHEIL, D. 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecology letters,* 12**,** 798-805.

BONILLA‐MOHENO, M. & HOLL, K. D. 2010. Direct Seeding to Restore Tropical Mature‐Forest Species in Areas of Slash‐and‐Burn Agriculture. *Restoration Ecology,* 18**,** 438-445.

BONNER, M. T. L., SCHMIDT, S. & SHOO, L. P. 2013. A meta-analytical global comparison of aboveground biomass accumulation between tropical secondary forests and monoculture plantations. *Forest Ecology and Management,* 291**,** 73-86.

BOUILLET, J.-P., LACLAU, J.-P., DE MORAES GONCALVES, J. L., VOIGTLAENDER, M., GAVA, J. L., LEITE, F. P., HAKAMADA, R., MARESCHAL, L., MABIALA, A. & TARDY, F. 2013. Eucalyptus and Acacia tree growth over entire rotation in single-and mixed-species plantations across five sites in Brazil and Congo. *Forest Ecology and Management,* 301**,** 89-101.

BREMER, L. L. & FARLEY, K. A. 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation,* 19**,** 3893-3915.

BREUGEL, M. V., HALL, J. S., CRAVEN, D. J., GREGOIRE, T. G., PARK, A., DENT, D. H., WISHNIE, M. H., MARISCAL, E., DEAGO, J., IBARRA, D., CEDEÑO, N. & ASHTON, M. S. 2011. Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. *Forest Ecology and Management,* 261**,** 1580-1589.

BRIENEN, R. J., PHILLIPS, O., FELDPAUSCH, T., GLOOR, E., BAKER, T., LLOYD, J., LOPEZ-GONZALEZ, G., MONTEAGUDO-MENDOZA, A., MALHI, Y. & LEWIS, S. 2015. Long-term decline of the Amazon carbon sink. *Nature,* 519**,** 344-348.

BROADBENT, E. N., ZAMBRANO, A. M. A., ASNER, G. P., SORIANO, M., FIELD, C. B., DE SOUZA, H. R., PEÑA-CLAROS, M., ADAMS, R. I., DIRZO, R. & GILES, L. 2014. Integrating stand and soil properties to understand foliar nutrient dynamics during forest succession following slash-and-burn agriculture in the Bolivian Amazon. *PloS one,* 9**,** e86042.

BRUEL, B. O., MARQUES, M. & BRITEZ, R. M. 2010. Survival and growth of tree species under two direct seedling planting systems. *Restoration Ecology,* 18**,** 414-417.

BRÜHL, C. A. & ELTZ, T. 2010. Fuelling the biodiversity crisis: species loss of ground-dwelling forest ants in oil palm plantations in Sabah, Malaysia (Borneo). *Biodiversity and Conservation,* 19**,** 519-529.

BRUIJNZEEL, L. A. 1990. Hydrology of moist tropical forests and effects of conversion: a state of knowledge review *UNESCO International Hydrological Programme.* Paris.

BRUIJNZEEL, L. A. 2004. Hydrological functions of tropical forests: not seeing the soil for the trees? *Agriculture, Ecosystems & Environment,* 104**,** 185-228.

BRYAN, J. E., SHEARMAN, P. L., ASNER, G. P., KNAPP, D. E., AORO, G. & LOKES, B. 2013. Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. *PloS one,* 8**,** e69679.

BUDIHARTA, S., MEIJAARD, E., ERSKINE, P. D., RONDININI, C., PACIFICI, M. & WILSON, K. A. 2014. Restoring degraded tropical forests for carbon and biodiversity. *Environmental Research Letters,* 9**,** 114020.

BULLOCK, J. M., ARONSON, J., NEWTON, A. C., PYWELL, R. F. & REY-BENAYAS, J. M. 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in Ecology & Evolution,* 26**,** 541-549.

BUSCHBACHER, R., UHL, C. & SERRAO, E. A. S. 1988. Abandoned Pastures in Eastern Amazonia. II. Nutrient Stocks in the Soil and Vegetation *Journal of ecology,* 76**,** 682-699.

BUSCHBACHER, R. J. 1986. Tropical deforestation and pasture development. *Bioscience,* 36**,** 22-28.

CAI, W., BORLACE, S., LENGAIGNE, M., VAN RENSCH, P., COLLINS, M., VECCHI, G., TIMMERMANN, A., SANTOSO, A., MCPHADEN, M. J., WU, L., ENGLAND, M. H., WANG, G., GUILYARDI, E. & JIN, F.-F. 2014. Increasing frequency of extreme El Nino events due to greenhouse warming. *Nature Clim. Change,* 4**,** 111-116.

CALVO-ALVARADO, J., ARIAS, D. & RICHTER, D. 2007. Early growth performance of native and introduced fast growing tree species in wet to sub-humid climates of the Southern region of Costa Rica. *Forest ecology and management,* 242**,** 227-235.

CAMARGO, J. L. C., FERRAZ, I. D. K. & IMAKAWA, A. M. 2002. Rehabilitation of Degraded Areas of Central Amazonia Using Direct Sowing of Forest Tree Seeds. *Restoration Ecology,* 10**,** 636-644.

CANADELL, J. G. & RAUPACH, M. R. 2008. Managing Forests for Climate Change Mitigation. *Science,* 320**,** 1456-1457.

CARDINALE, B. J., DUFFY, J. E., GONZALEZ, A., HOOPER, D. U., PERRINGS, C., VENAIL, P., NARWANI, A., MACE, G. M., TILMAN, D. & WARDLE, D. A. 2012. Biodiversity loss and its impact on humanity. *Nature,* 486**,** 59-67.

CARDINALE, B. J., MATULICH, K. L., HOOPER, D. U., BYRNES, J. E., DUFFY, E., GAMFELDT, L., BALVANERA, P., O'CONNOR, M. I. & GONZALEZ, A. 2011. The functional role of producer diversity in ecosystems. *American Journal of Botany,* 98**,** 572-592.

CARPENTER, NICHOLS & EDUER 2004a. Early growth of native and exotic trees planted on degraded tropical pasture. *Forest Ecology and Management,* 196**,** 367-378.

CARPENTER, NICHOLS, PRATT & YOUNG 2004b. Methods of facilitating reforestation of tropical degraded land with the native timber tree *Terminalia amazonia*. *Forest Ecology and Management,* 202**,** 281-291.

CATFORD, J. A., DAEHLER, C. C., MURPHY, H. T., SHEPPARD, A. W., HARDESTY, B. D., WESTCOTT, D. A., REJMÁNEK, M., BELLINGHAM, P. J., PERGL, J., HORVITZ, C. C. & HULME, P. E. 2012. The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics,* 14**,** 231-241.

CATTERALL, C. P., FREEMAN, A. N., KANOWSKI, J. & FREEBODY, K. 2012. Can active restoration of tropical rainforest rescue biodiversity? A case with bird community indicators. *Biological Conservation,* 146**,** 53-61.

CBD 2011. Strategic plan for biodiversity 2011-2020 and the Aichi targets http://www.cbd.int/doc/strategic-plan/2011-2020/Aichi-Targets-EN.pdf. Montreal, Canada: Convention on Biological Diversity.

CBD 2013. Quick guides to the Aichi Biodiversity Targets. Convention on Biological Diversity.

CÉSAR, R. G., HOLL, K. D., GIRÃO, V. J., MELLO, F. N. A., VIDAL, E., ALVES, M. C. & BRANCALION, P. H. S. 2016. Evaluating climber cutting as a strategy to restore degraded tropical forests. *Biological Conservation,* 201**,** 309-313.

CHAER, G. M., RESENDE, A. S., CAMPELLO, E. F. C., DE FARIA, S. M. & BODDEY, R. M. 2011. Nitrogen-fixing legume tree species for the reclamation of severely degraded lands in Brazil. *Tree Physiology,* 31**,** 139-149.

CHAMBERS, J. Q., HIGUCHI, N., SCHIMEL, J. P., FERREIRA, L. V. & MELACK, J. M. 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia,* 122**,** 380-388.

CHAPMAN, C. & CHAPMAN, L. 1999. Forest Restoration in Abandoned Agricultural Land: a Case Study from East Africa. *Conservation biology,* 13**,** 1301-1311.

CHAPMAN, C. A. & LAMBERT, J. E. 2000. Habitat alteration and the conservation of African primates: Case study of Kibale National Park, Uganda. *American Journal of Primatology,* 50**,** 169-185.

CHAVE, J., CONDIT, R., LAO, S., CASPERSEN, J. P., FOSTER, R. B. & HUBBELL, S. P. 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *Journal of Ecology,* 91**,** 240-252.

CHAVE, J., MULLER-LANDAU, H. C., BAKER, T. R., EASDALE, T. A., TER STEEGE, H. & WEBB, C. O. 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications,* 16**,** 2356-2367.

CHAVE, J., RÉJOU-MÉCHAIN, M., BÚRQUEZ, A., CHIDUMAYO, E., COLGAN, M. S., DELITTI, W. B. C., DUQUE, A., EID, T., FEARNSIDE, P. M., GOODMAN, R. C., HENRY, M., MARTÍNEZ-YRÍZAR, A., MUGASHA, W. A., MULLER-LANDAU, H. C., MENCUCCINI,

M., NELSON, B. W., NGOMANDA, A., NOGUEIRA, E. M., ORTIZ-MALAVASSI, E., PÉLISSIER, R., PLOTON, P., RYAN, C. M., SALDARRIAGA, J. G. & VIEILLEDENT, G. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology,* 20**,** 3177-3190.

CHAZDON, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, evolution and systematics,* 6**,** 51-71.

CHAZDON, R. L. 2008. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science,* 320**,** 1458-1460.

CHAZDON, R. L. 2014. *Second growth: the promise of tropical forest regeneration in an age of deforestation*, University of Chicago Press.

CHAZDON, R. L., BRANCALION, P. H., LAMB, D., LAESTADIUS, L., CALMON, M. & KUMAR, C. 2015. A Policy‐Driven Knowledge Agenda for Global Forest and Landscape Restoration. *Conservation Letters*.

CHAZDON, R. L., BRANCALION, P. H. S., LAESTADIUS, L., BENNETT-CURRY, A., BUCKINGHAM, K., KUMAR, C., MOLL-ROCEK, J., VIEIRA, I. C. G. & WILSON, S. J. 2016a. When is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. *Ambio***,** 1-13.

CHAZDON, R. L., BROADBENT, E. N., ROZENDAAL, D. M., BONGERS, F., ZAMBRANO, A. M. A., AIDE, T. M., BALVANERA, P., BECKNELL, J. M., BOUKILI, V. & BRANCALION, P. H. 2016b. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances,* 2.

CHAZDON, R. L., REDONDO BRENES, A. & VILCHEZ ALVARADO, B. 2005. Effects of climate and stand age on annual tree dynamics in tropical second‐growth rain forests. *Ecology,* 86**,** 1808-1815.

CHAZDON, R. L. & URIARTE, M. 2016. Natural regeneration in the context of large‐scale forest and landscape restoration in the tropics. *Biotropica,* 48**,** 709-715.

CHEN, I., HILL, J. K., SHIU, H. J., HOLLOWAY, J. D., BENEDICK, S., CHEY, V. K., BARLOW, H. S. & THOMAS, C. D. 2011a. Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography,* 20**,** 34-45.

CHEN, I.-C., HILL, J. K., OHLEMÜLLER, R., ROY, D. B. & THOMAS, C. D. 2011b. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science,* 333**,** 1024-1026.

CHISHOLM, R. A., MULLER-LANDAU, H. C., ABDUL RAHMAN, K., BEBBER, D. P., BIN, Y., BOHLMAN, S. A., BOURG, N. A., BRINKS, J., BUNYAVEJCHEWIN, S., BUTT, N., CAO, H., CAO, M., CÁRDENAS, D., CHANG, L.-W., CHIANG, J.-M., CHUYONG, G., CONDIT, R., DATTARAJA, H. S., DAVIES, S., DUQUE, A., FLETCHER, C., GUNATILLEKE, N., GUNATILLEKE, S., HAO, Z., HARRISON, R. D., HOWE, R., HSIEH, C.-F., HUBBELL, S. P., ITOH, A., KENFACK, D., KIRATIPRAYOON, S., LARSON, A. J., LIAN, J., LIN, D., LIU, H., LUTZ, J. A., MA, K., MALHI, Y., MCMAHON, S., MCSHEA, W., MEEGASKUMBURA, M., MOHD. RAZMAN, S., MORECROFT, M. D., NYTCH, C. J., OLIVEIRA, A., PARKER, G. G., PULLA, S., PUNCHI-MANAGE, R., ROMERO-SALTOS, H., SANG, W., SCHURMAN, J., SU, S.-H., SUKUMAR, R., SUN, I. F., SURESH, H. S., TAN, S., THOMAS, D., THOMAS, S., THOMPSON, J., VALENCIA, R., WOLF, A., YAP, S., YE, W., YUAN, Z. & ZIMMERMAN, J. K. 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology,* 101**,** 1214-1224.

CIFOR 2004. Site Management and Productivity in Tropical Plantation Forests. *In:* NAMBIAL, E. K. S., RANGER, J., TIARKS, A. & TOMA, T. (eds.) *Proceedings of Workshops in Congo July 2001 and China February 2003.* Indonesia: CIFOR.

CIFUENTES-JARA, M. 2008. *Aboveground biomass and ecosystem carbon pools in tropical secondary forests growing in six life zones of Costa Rica*, ProQuest.

CINCOTTA, R., WISNEWSKI, J. & ENGELMAN, R. 2000. Human population in the biodiversity hotspots. *Nature,* 404**,** 990-992.
COCHRANE, M. A. 2003. Fire science for rainforests. *Nature,* 421**,** 913-919.
COCHRANE, M. A., ALENCAR, A., SCHULZE, M. D., SOUZA, C. M., NEPSTAD, D. C., LEFEBVRE, P. & DAVIDSON, E. A. 1999. Positive Feedbacks in the Fire Dynamic of Closed Canopy Tropical Forests. *Science,* 284**,** 1832-1835.
COCHRANE, M. A. & LAURANCE, W. F. 2002. Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology,* 18**,** 311-325.
CONDIT, R. 1998. *Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots*, Springer Science & Business Media.
CONDIT, R., AGUILAR, S., HERNANDEZ, A., PEREZ, R., LAO, S., ANGEHR, G., HUBBELL, S. P. & FOSTER, R. B. 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Nino dry season. *Journal of Tropical Ecology,* 20**,** 51-72.
CONDIT, R., PITMAN, N., LEIGH, E. G., CHAVE, J., TERBORGH, J., FOSTER, R. B., NÚÑEZ, P., AGUILAR, S., VALENCIA, R., VILLA, G., MULLER-LANDAU, H. C., LOSOS, E. & HUBBELL, S. P. 2002. Beta-Diversity in Tropical Forest Trees. *Science,* 295**,** 666-669.
CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science,* 199**,** 1302-1310.
CORLEY, R., HARDON, J. & TAN, G. 1971. Analysis of growth of the oil palm (Elaeis guineensis Jacq.) I. Estimation of growth parameters and application in breeding. *Euphytica,* 20**,** 307-315.
CORLEY, R. H. V. & TINKER, P. 2008. *The oil palm*, John Wiley & Sons.
COSTA, L. G. S., MIRANDA, I. S., GRIMALDI, M., SILVA, M. L., MITJA, D. & LIMA, T. T. S. 2012. Biomass in different types of land use in the Brazil's 'arc of deforestation'. *Forest Ecology and Management,* 278**,** 101-109.
COSTANZA, R., D'ARGE, R., GROOT, R. D., FARBER, S., GRASSO, M., HANNON, B., LIMBURG, K., NAEEM, S., O'NEILL, R. V. & PARUELO, J. 1998. The value of the world's ecosystem services and natural capital.
CRAWLEY, M. J. 2012. *The R book*, John Wiley & Sons.
CROUZEILLES, R., CURRAN, M., FERREIRA, M. S., LINDENMAYER, D. B., GRELLE, C. E. & BENAYAS, J. M. R. 2016. A global meta-analysis on the ecological drivers of forest restoration success. *Nature communications,* 7.
CTFS. 2016. *Center for Tropical Forest Science and Forest Global Earth Observatories (CTFS-ForestGEO)* http://www.ctfs.si.edu/group/About/ [Online]. [accessed September 2015].
CUBIÑA, A. & AIDE, T. M. 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica,* 33**,** 260-267.
D'OLIVEIRA, M. V. N., ALVARADO, E. C., SANTOS, J. C. & CARVALHO, J. A. 2011. Forest natural regeneration and biomass production after slash and burn in a seasonally dry forest in the Southern Brazilian Amazon. *Forest Ecology and Management,* 261**,** 1490-1498.
DAVIDSON, E. A. & MARTINELLI, L. A. 2009. Nutrient Limitations to Secondary Forest Regrowth. *In:* KELLER, M., BUSTAMANTE, M., GASH, J. & DIAS, P. S. (eds.) *Amazonia and Global Change.* Washington: Amer Geophysical Union.
DAVIDSON, E. A., REIS DE CARVALHO, C. J., VIEIRA, I., FIGUEIREDO, R. D., MOUTINHO, P., ISHIDA, F. Y., PRIMO DOS SANTOS, M., GUERRERO, J., KALIF, K. & SABÁ, R. 2004. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecological applications,* 14**,** S150-S163.
DE JONG, B. H. J. 2001. Uncertainties in estimating the potential for carbon mitigation of forest management. *Forest Ecology and Management,* 154**,** 85-104.

DE SOUZA, F. M. & BATISTA, J. L. F. 2004. Restoration of seasonal semideciduous forests in Brazil: influence of age and restoration design on forest structure. *Forest Ecology and Management,* 191**,** 185-200.

DEANS, J. D., MORAN, J. & GRACE, J. 1996. Biomass relationships for tree species in regenerating semi-deciduous tropical moist forest in Cameroon. *Forest Ecology and Management,* 88**,** 215-225.

DEFRIES, R., ACHARD, F., BROWN, S., HEROLD, M., MURDIYARSO, D., SCHLAMADINGER, B. & DE SOUZA JR, C. 2007. Earth observations for estimating greenhouse gas emissions from deforestation in developing countries. *Environmental Science & Policy,* 10**,** 385-394.

DEFRIES, R. S., RUDEL, T., URIARTE, M. & HANSEN, M. 2010. Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience,* 3**,** 178-181.

DEL AGUILA-PASQUEL, J., DOUGHTY, C. E., METCALFE, D. B., SILVA-ESPEJO, J. E., GIRARDIN, C. A., CHUNG GUTIERREZ, J. A., NAVARRO-AGUILAR, G. E., QUESADA, C. A., HIDALGO, C. G. & REYNA HUAYMACARI, J. M. 2014. The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru). *Plant Ecology & Diversity,* 7**,** 71-83.

DELAGRANGE, S., POTVIN, C., MESSIER, C. & COLL, L. 2008. Linking multiple-level tree traits with biomass accumulation in native tree species used for reforestation in Panama. *Trees,* 22**,** 337-349.

DENSLOW, J. S. & GUZMAN, G. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science,* 11**,** 201-212.

DIAS, A. T., BOZELLI, R. L., DARIGO, R. M., ESTEVES, F. D. A., DOS SANTOS, H. F., FIGUEIREDO‐BARROS, M. P., NUNES, M. F. Q., ROLAND, F., ZAMITH, L. R. & SCARANO, F. R. 2012. Rehabilitation of a Bauxite Tailing Substrate in Central Amazonia: The Effect of Litter and Seed Addition on Flood‐Prone Forest Restoration. *Restoration Ecology,* 20**,** 483-489.

DIAZ-BALTEIRO, L. & RODRIGUEZ, L. C. E. 2006. Optimal rotations on Eucalyptus plantations including carbon sequestration—A comparison of results in Brazil and Spain. *Forest Ecology and Management,* 229**,** 247-258.

DIRZO, R. & RAVEN, P. H. 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources,* 28**,** 137-167.

DOAK, D. F., BIGGER, D., HARDING, E. K., MARVIER, M. A., O'MALLEY, R. E. & THOMSON, D. 1998. The Statistical Inevitability of Stability‐Diversity Relationships in Community Ecology. *The American Naturalist,* 151**,** 264-276.

DOHRMANN, R. 2006. Cation exchange capacity methodology II: A modified silver–thiourea method. *Applied Clay Science,* 34**,** 38-46.

DON, A., SCHUMACHER, J. & FREIBAUER, A. 2011. Impact of tropical land-use change on soil organic carbon stocks – a meta-analysis. *Global Change Biology,* 17**,** 1658-1670.

DONATO, D. C., KAUFFMAN, J. B., MURDIYARSO, D., KURNIANTO, S., STIDHAM, M. & KANNINEN, M. 2011. Mangroves among the most carbon-rich forests in the tropics. *Nature Geosci,* 4**,** 293-297.

DOUGLAS, I., GREER, T., BIDIN, K. & SPILSBURY, M. 1993. Impacts of Rainforest Logging on River Systems and Communities in Malaysia and Kalimantan. *Global Ecology and Biogeography Letters,* 3**,** 245-252.

DOUST, S. J., ERSKINE, P. D. & LAMB, D. 2008. Restoring rainforest species by direct seeding: tree seedling establishment and growth performance on degraded land in the wet tropics of Australia. *Forest Ecology and Management,* 256**,** 1178-1188.

DUPUY, J. M. & CHAZDON, R. L. 1998. Long-term effects of forest regrowth and selective logging on the seed bank of tropical forests in NE Costa Rica. *Biotropica,* 30**,** 223-237.

DUPUY, J. M., HERNÁNDEZ‐STEFANONI, J. L., HERNÁNDEZ‐JUÁREZ, R. A., TETETLA‐RANGEL, E., LÓPEZ‐MARTÍNEZ, J. O., LEYEQUIÉN‐ABARCA, E., TUN‐DZUL, F. J. & MAY‐PAT, F. 2012. Patterns and correlates of tropical dry forest structure and composition in a highly replicated chronosequence in Yucatan, Mexico. *Biotropica,* 44**,** 151-162.

DZULKIFLI , D. 2014. Effects of two major forest restoration regimes on the growth and survival of seedlings of 16 Dipterocarp species. *The Effects of Forest Management Practices on Forest Regeneration and Arthropod Diversity.* University of Zurich, PhD thesis, 43-76: Faculty of Mathematics and Natural Sciences.

EATON, J. M. & LAWRENCE, D. 2009. Loss of carbon sequestration potential after several decades of shifting cultivation in the Southern Yucatan. *Forest Ecology and Management,* 258**,** 949-958.

EDWARDS, D. P., ANCELL, F. A., AHMAD, A. H., NILUS, R. & HAMER, K. C. 2009. The value of rehabilitating logged rainforest for birds. *Conservation Biology,* 23**,** 1628-1633.

EDWARDS, D. P., BACKHOUSE, A. R., WHEELER, C., KHEN, C. V. & HAMER, K. C. 2012. Impacts of logging and rehabilitation on invertebrate communities in tropical rainforests of northern Borneo. *Journal of Insect Conservation,* 16**,** 591-599.

EDWARDS, D. P., HODGSON, J. A., HAMER, K. C., MITCHELL, S. L., AHMAD, A. H., CORNELL, S. J. & WILCOVE, D. S. 2010. Wildlife‐friendly oil palm plantations fail to protect biodiversity effectively. *Conservation Letters,* 3**,** 236-242.

EDWARDS, D. P., LARSEN, T. H., DOCHERTY, T. D. S., ANSELL, F. A., HSU, W. W., DERHÉ, M. A., HAMER, K. C. & WILCOVE, D. S. 2011. Degraded lands worth protecting: the biological importance of Southeast Asia's repeatedly logged forests. *Proceedings of the Royal Society B: Biological Sciences,* 278**,** 82-90.

EHIGIATOR, O. A. & ANYATA, B. U. 2011. Effects of land clearing techniques and tillage systems on runoff and soil erosion in a tropical rain forest in Nigeria. *Journal of environmental management,* 92**,** 2875-2880.

ELTON, C. S. 1958. *The ecology of invasions by animals and plants* London, Methuen.

EPRON, D., NOUVELLON, Y., MARESCHAL, L., E MOREIRA, R. M., KOUTIKA, L.-S., GENESTE, B., DELGADO-ROJAS, J. S., LACLAU, J.-P., SOLA, G. & DE MORAES GONCALVES, J. L. 2013. Partitioning of net primary production in Eucalyptus and Acacia stands and in mixed-species plantations: two case-studies in contrasting tropical environments. *Forest Ecology and Management,* 301**,** 102-111.

ERSKINE, P. D., LAMB, D. & BRISTOW, M. 2006. Tree species diversity and ecosystem function: Can tropical multi-species plantations generate greater productivity? *Forest Ecology and Management,* 233**,** 205-210.

EVA, H. D., ACHARD, F., BEUCHLE, R., DE MIRANDA, E., CARBONI, S., SELIGER, R., VOLLMAR, M., HOLLER, W. A., OSHIRO, O. T. & BARRENA ARROYO, V. 2012. Forest cover changes in tropical South and Central America from 1990 to 2005 and related carbon emissions and removals. *Remote Sensing,* 4**,** 1369-1391.

EWEL, J., CHAI, P. & LIM, M. 1983. Biomass and floristics of three young second-growth forests in Sarawak. *Malay. For,* 46**,** 347-64.

FABIÃO, A., MADEIRA, M., STEEN, E., KÄTTERER, T., RIBEIRO, C. & ARAÚJO, C. 1995. Development of root biomass in an Eucalyptus globulus plantation under different water and nutrient regimes. *Nutrient Uptake and Cycling in Forest Ecosystems.* Springer.

FAJARDO, L., RODRIGUEZ, J., GONZALEZ, V. & BRICENO-LINARES, J. 2013. Restoration of a degraded tropical dry forest in Macanao, Venezuela. *Journal of Arid Environments,* 88**,** 236-243.

FAO 1993. Proceedings, Regional Expert Consultation of Eucalyptus. *In:* WHITE, K., BALL, J. & KASHIO, M. (eds.) *RAPA Publication.* Bangkok, Thailand: FAO.

FAO 1999. Towards a harmonized definition of non-wood forest products. *Non-wood Forest Products and Income Generation.* Unasylva No 198.

FAO 2000. On definitions of forest and forest change *Forest Resources Assessment working paper 33.* Rome.

FAO 2009. State of the worlds forests 2009. Rome: Food and Agricultural Organization of the United Nations.

FAO 2010. Global Forest Resources Assessment 2010. *FAO Forestry paper 163.* Rome.

FAO 2011. State of the worlds forests 2011. Rome: Food and Agricultural Organization of the United Nations.

FAOSTAT. 2014. *FAOSTAT online statistical service* [Online]. Rome, Italy. Available: http://faostat.fao.org/ [Accessed 29/10/14.

FEARNSIDE, P. M. & GUIMARÃES, W. M. 1996. Carbon uptake by secondary forests in Brazilian Amazonia. *Forest Ecology and Management,* 80**,** 35-46.

FEHSE, J., HOFSTEDE, R., AGUIRRE, N., PALADINES, C., KOOIJMAN, A. & SEVINK, J. 2002. High altitude tropical secondary forests: a competitive carbon sink? *Forest Ecology and Management,* 163**,** 9-25.

FELDPAUSCH, T., FELDPAUSCH, T. R., PRATES-CLARK, C. D. C., RIHA, S. & RIHA, S. J. 2007. Secondary forest growth deviation from chronosequence predictions in central Amazonia. *Global change biology,* 13**,** 967-979.

FELDPAUSCH, T. R., BANIN, L., PHILLIPS, O. L., BAKER, T. R., LEWIS, S. L., QUESADA, C. A., AFFUM-BAFFOE, K., ARETS, E., BERRY, N. J., BIRD, M., BRONDIZIO, E. S., DE CAMARGO, P., CHAVE, J., DJAGBLETEY, G., DOMINGUES, T. F., DRESCHER, M., FEARNSIDE, P. M., FRANCA, M. B., FYLLAS, N. M., LOPEZ-GONZALEZ, G., HLADIK, A., HIGUCHI, N., HUNTER, M. O., IIDA, Y., SALIM, K. A., KASSIM, A. R., KELLER, M., KEMP, J., KING, D. A., LOVETT, J. C., MARIMON, B. S., MARIMON, B. H., LENZA, E., MARSHALL, A. R., METCALFE, D. J., MITCHARD, E. T. A., MORAN, E. F., NELSON, B. W., NILUS, R., NOGUEIRA, E. M., PALACE, M., PATINO, S., PEH, K. S. H., RAVENTOS, M. T., REITSMA, J. M., SAIZ, G., SCHRODT, F., SONKE, B., TAEDOUMG, H. E., TAN, S., WHITE, L., WOLL, H. & LLOYD, J. 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences,* 8**,** 1081-1106.

FELDPAUSCH, T. R., LLOYD, J., LEWIS, S. L., BRIENEN, R. J. W., GLOOR, M., MENDOZA, A. M., LOPEZ-GONZALEZ, G., BANIN, L., ABU SALIM, K., AFFUM-BAFFOE, K., ALEXIADES, M., ALMEIDA, S., AMARAL, I., ANDRADE, A., ARAGAO, L., MURAKAMI, A. A., ARETS, E., ARROYO, L., AYMARD, G. A., BAKER, T. R., BANKI, O. S., BERRY, N. J., CARDOZO, N., CHAVE, J., COMISKEY, J. A., ALVAREZ, E., DE OLIVEIRA, A., DI FIORE, A., DJAGBLETEY, G., DOMINGUES, T. F., ERWIN, T. L., FEARNSIDE, P. M., FRANCA, M. B., FREITAS, M. A., HIGUCHI, N., HONORIO, E., IIDA, Y., JIMENEZ, E., KASSIM, A. R., KILLEEN, T. J., LAURANCE, W. F., LOVETT, J. C., MALHI, Y., MARIMON, B. S., MARIMON, B. H., LENZA, E., MARSHALL, A. R., MENDOZA, C., METCALFE, D. J., MITCHARD, E. T. A., NEILL, D. A., NELSON, B. W., NILUS, R., NOGUEIRA, E. M., PARADA, A., PEH, K. S. H., CRUZ, A. P., PENUELA, M. C., PITMAN, N. C. A., PRIETO, A., QUESADA, C. A., RAMIREZ, F., RAMIREZ-ANGULO, H., REITSMA, J. M., RUDAS, A., SAIZ, G., SALOMAO, R. P., SCHWARZ, M., SILVA, N., SILVA-ESPEJO, J. E., SILVEIRA, M., SONKE, B., STROPP, J., TAEDOUMG, H. E., TAN, S., TER STEEGE, H., TERBORGH, J., TORELLO-RAVENTOS, M., VAN DER HEIJDEN, G. M. F., VASQUEZ, R., VILANOVA, E., VOS, V. A., WHITE, L., WILLCOCK, S., WOELL, H. & PHILLIPS, O. L. 2012. Tree

height integrated into pantropical forest biomass estimates. *Biogeosciences,* 9**,** 3381-3403.
FINEGAN, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends in Ecology & Evolution,* 11**,** 119-124.
FISHER, B. 2010. African exception to drivers of deforestation. *Nature Geoscience,* 3**,** 375-376.
FISHER, B., EDWARDS, D. P., GIAM, X. L. & WILCOVE, D. S. 2011. The high costs of conserving Southeast Asia's lowland rainforests. *Frontiers in Ecology and the Environment,* 9**,** 329-334.
FISHER, J. B., SIKKA, M., SITCH, S., CIAIS, P., POULTER, B., GALBRAITH, D., LEE, J.-E., HUNTINGFORD, C., VIOVY, N., ZENG, N., AHLSTRÖM, A., LOMAS, M. R., LEVY, P. E., FRANKENBERG, C., SAATCHI, S. & MALHI, Y. 2013. African tropical rainforest net carbon dioxide fluxes in the twentieth century. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 368.
FITZHERBERT, E. B., STRUEBIG, M. J., MOREL, A., DANIELSEN, F., BRÜHL, C. A., DONALD, P. F. & PHALAN, B. 2008. How will oil palm expansion affect biodiversity? *Trends in ecology & evolution,* 23**,** 538-545.
FONSECA, W., BENAYAS, J. M. R. & ALICE, F. E. 2011. Carbon accumulation in the biomass and soil of different aged secondary forests in the humid tropics of Costa Rica. *Forest Ecology and Management,* 262**,** 1400-1408.
FOX, J. 2000. How blaming'slash and burn'farmers is deforesting mainland Southeast Asia. *Analysis from the East-West Center*
No. 47.
FRIEDLINGSTEIN, P., ANDREW, R. M., ROGELJ, J., PETERS, G. P., CANADELL, J. G., KNUTTI, R., LUDERER, G., RAUPACH, M. R., SCHAEFFER, M., VAN VUUREN, D. P. & LE QUERE, C. 2014. Persistent growth of CO2 emissions and implications for reaching climate targets. *Nature Geosci,* 7**,** 709-715.
FUI YEE, L. 2006. *Factors affecting tree seedling establishment following rehabilitation management in logged-over tropical rainforest in Sabah, Malaysia.* Doctor of Philosophy, University of London.
FUKUSHIMA, M., KANZAKI, M., HARA, M., OHKUBO, T., PREECHAPANYA, P. & CHOOCHAROEN, C. 2008. Secondary forest succession after the cessation of swidden cultivation in the montane forest area in Northern Thailand. *Forest Ecology and Management,* 255**,** 1994-2006.
FUKUSHIMA, M., KANZAKI, M., THEIN, H. & MINN, Y. 2007. Recovery process of fallow vegetation in the traditional Karen swidden cultivation system in the Bago mountain range, Myanmar. *SOUTH EAST ASIAN STUDIES,* 45**,** 317.
FULLER, D., JESSUP, T. & SALIM, A. 2004. Loss of forest cover in Kalimantan, Indonesia, since the 1997–1998 El Nino. *Conservation Biology,* 18**,** 249-254.
GALBRAITH, D., MALHI, Y., AFFUM-BAFFOE, K., CASTANHO, A. D., DOUGHTY, C. E., FISHER, R. A., LEWIS, S. L., PEH, K. S.-H., PHILLIPS, O. L. & QUESADA, C. A. 2013. Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity,* 6**,** 139-157.
GARDNER, T. A., BARLOW, J., CHAZDON, R., EWERS, R. M., HARVEY, C. A., PERES, C. A. & SODHI, N. S. 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters,* 12**,** 561-582.
GEHRING, C., DENICH, M. & VLEK, P. L. G. 2005. Resilience of secondary forest regrowth after slash-and-burn agriculture in central Amazonia. *Journal of Tropical Ecology,* 21**,** 519-527.
GEIST, H. J. & LAMBIN, E. F. 2002. Proximate Causes and Underlying Driving Forces of Tropical Deforestation. *BioScience,* 52**,** 143-150.
GELMAN, A. & HILL, J. 2006. *Data analysis using regression and multilevel/hierarchical models*, Cambridge University Press.

GENTRY, A. H. 1988. Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America,* 85**,** 156-159.
GENTRY, A. H. & DODSON, C. 1987. Contribution of Nontrees to Species Richness of a Tropical Rain Forest. *Biotropica,* 19**,** 149-156.
GERWING, J. J. 2002. Degradation of forests through logging and fire in the eastern Brazilian Amazon. *Forest Ecology and Management,* 157**,** 131-141.
GIBSON, L., LEE, T. M., KOH, L. P., BROOK, B. W., GARDNER, T. A., BARLOW, J., PERES, C. A., BRADSHAW, C. J., LAURANCE, W. F. & LOVEJOY, T. E. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature,* 478**,** 378-381.
GILROY, J. J., WOODCOCK, P., EDWARDS, F. A., WHEELER, C., BAPTISTE, B. L., URIBE, C. A. M., HAUGAASEN, T. & EDWARDS, D. P. 2014. Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. *CAB reviews: perspectives in agriculture, veterinary science, nutrition and natural resources*.
GOFC-GOLD 2015. A sourcebook of methods and procedures for monitoring and reporting anthropogenic greenhouse gas emissions and removals associated with deforestation, gains and losses of carbon stocks in forests remaining forests, and forestation. *GOFC-GOLD Report version COP21-1.* The Netherlands: Wageningen University.
GOURLET-FLEURY, S., MORTIER, F., FAYOLLE, A., BAYA, F., OUÉDRAOGO, D., BÉNÉDET, F. & PICARD, N. 2013. Tropical forest recovery from logging: a 24 year silvicultural experiment from Central Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 368.
GRACE, J. 2004. Understanding and managing the global carbon cycle. *Journal of Ecology,* 92**,** 189-202.
GRACE, J., MITCHARD, E. & GLOOR, E. 2014. Perturbations in the carbon budget of the tropics. *Global Change Biology,* 20**,** 3238-3255.
GRANT, J. C., NICHOLS, J. D., PELLETIER, M.-C., GLENCROSS, K. & BELL, R. 2006. Five year results from a mixed-species spacing trial with six subtropical rainforest tree species. *Forest Ecology and Management,* 233**,** 309-314.
GUAN, K., PAN, M., LI, H., WOLF, A., WU, J., MEDVIGY, D., CAYLOR, K. K., SHEFFIELD, J., WOOD, E. F., MALHI, Y., LIANG, M., KIMBALL, J. S., SALESKA, S. R., BERRY, J., JOINER, J. & LYAPUSTIN, A. I. 2015. Photosynthetic seasonality of global tropical forests constrained by hydroclimate. *Nature Geosci,* 8**,** 284-289.
GUARIGUATA, M. R., GARCÍA-FERNÁNDEZ, C., SHEIL, D., NASI, R., HERRERO-JÁUREGUI, C., CRONKLETON, P. & INGRAM, V. 2010. Compatibility of timber and non-timber forest product management in natural tropical forests: Perspectives, challenges, and opportunities. *Forest Ecology and Management,* 259**,** 237-245.
GUARIGUATA, M. R. & OSTERTAG, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management,* 148**,** 185-206.
GUARINO, E. D. S. G. & SCARIOT, A. O. 2012. Tree seedling survival and growth in logged and undisturbed seasonal deciduous forest fragments in central Brazil. *Journal of Forest Research,* 17**,** 193-201.
GUILLAUME, T., HOLTKAMP, A. M., DAMRIS, M., BRÜMMER, B. & KUZYAKOV, Y. 2016. Soil degradation in oil palm and rubber plantations under land resource scarcity. *Agriculture, Ecosystems & Environment,* 232**,** 110-118.
HAMILTON, A. J., BASSET, Y., BENKE, K. K., GRIMBACHER, P. S., MILLER, S. E., NOVOTNÝ, V., SAMUELSON, G. A., STORK, N. E., WEIBLEN, G. D. & YEN, J. D. 2010. Quantifying uncertainty in estimation of tropical arthropod species richness. *The American Naturalist,* 176**,** 90-95.
HANSEN, M. C., POTAPOV, P. V., MOORE, R., HANCHER, M., TURUBANOVA, S. A., TYUKAVINA, A., THAU, D., STEHMAN, S. V., GOETZ, S. J., LOVELAND, T. R.,

KOMMAREDDY, A., EGOROV, A., CHINI, L., JUSTICE, C. O. & TURUBANOVA, S. A. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science,* 342**,** 850-853.

HARTEMINK, A. E. 2001. Biomass and nutrient accumulation of *Piper aduncum* and *Imperata cylindrica* fallows in the humid lowlands of Papua New Guinea. *Forest Ecology and Management,* 144**,** 19-32.

HASHIMOTIO, T., KOJIMA, K., TANGE, T. & SASAKI, S. 2000. Changes in carbon storage in fallow forests in the tropical lowlands of Borneo. *Forest Ecology and Management,* 126**,** 331-337.

HATTORI, D., KENZO, T., IRINO, K. O., KENDAWANG, J. J., NINOMIYA, I. & SAKURAI, K. 2013. Effects of soil compaction on the growth and mortality of planted dipterocarp seedlings in a logged-over tropical rainforest in Sarawak, Malaysia. *Forest Ecology and Management,* 310**,** 770-776.

HECTOR, A., PHILIPSON, C., SANER, P., CHAMAGNE, J., DZULKIFLI, D., O'BRIEN, M., SNADDON, J. L., ULOK, P., WEILENMANN, M. & REYNOLDS, G. 2011. The Sabah Biodiversity Experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 366**,** 3303-3315.

HERTEL, D., MOSER, G., CULMSEE, H., ERASMI, S., HORNA, V., SCHULDT, B. & LEUSCHNER, C. 2009. Below- and above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi, Indonesia) as compared to neotropical forests. *Forest Ecology and Management,* 258**,** 1904-1912.

HIJMANS, R. J., CAMERON, S. E., PARRA, J. L., JONES, P. G. & JARVIS, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology,* 25**,** 1965-1978.

HILL, J. K., GRAY, M. A., KHEN, C. V., BENEDICK, S., TAWATAO, N. & HAMER, K. C. 2011. Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? *Philosophical Transactions of the Royal Society B: Biological Sciences,* 366**,** 3265-3276.

HILL, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology,* 54**,** 427-432.

HOBBS, R. J. & HUENNEKE, L. F. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation biology,* 6**,** 324-337.

HODGSON, J. A., THOMAS, C. D., WINTLE, B. A. & MOILANEN, A. 2009. Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology,* 46**,** 964-969.

HOLL, K. D. 1999. Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture: Seed Rain, Seed Germination, Microclimate, and Soil. *Biotropica,* 31**,** 229-242.

HOLL, K. D., ZAHAWI, R. A., COLE, R. J., OSTERTAG, R. & CORDELL, S. 2011. Planting Seedlings in Tree Islands Versus Plantations as a Large‐Scale Tropical Forest Restoration Strategy. *Restoration Ecology,* 19**,** 470-479.

HOLM, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics***,** 65-70.

HOOPER, D., CHAPIN III, F., EWEL, J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J., LODGE, D., LOREAU, M. & NAEEM, S. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs,* 75**,** 3-35.

HOOPER, E., CONDIT, R. & LEGENDRE, P. 2002. Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. *Ecological Applications,* 12**,** 1626-1641.

HOUGHTON, R., BYERS, B. & NASSIKAS, A. A. 2015. A role for tropical forests in stabilizing atmospheric CO2. *Nature Climate Change,* 5**,** 1022-1023.
HUBBELL, S. P. 2006. Neutral theory and the evolution of ecological equivalence. *Ecology,* 87**,** 1387-1398.
HUGHES, R. F., KAUFFMAN, J. B. & JARAMILLO, V. J. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology,* 80**,** 1892-1907.
IPCC 2006a. IPCC Good Practice Guidance for Land Use, Land-Use Change and Forestry. *In:* PENMAN, J., GYTARSKY, M., HIRAISHI, T., KRUG, T., KRUGER, D., PIPATTI, R., BUENDIA, L., MIWA, K., NGARA, T., TANABE, K. & WAGNER, F. (eds.). Kanagawa, Japan: Intergovernmental Panel on Climate Change.
IPCC 2006b. IPCC Guidelines for National Greenhouse Gas Inventories *In:* EGGLESTON, S., BUENDIA, L., MIWA, K., NGARA, T. & TANABE, K. (eds.) *Agriculture, Forestry and Other Land Use.* Intergovernmental Panel on Climate Change.
IPCC 2013. Climate Change 2013: The Physical Science Basis. *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, United Kingdom.
IPCC 2014. Climate Change 2014: Mitigation of Climate Change. *Working group III.* Intergovernmental Panel on Climate Change.
ITTO 2002. ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests. *ITTO Policy Development Series* International Tropical Timber Organization.
ITTO 2012. Annual review and assessment of the world timber situation. *International Tropical Timber Organization.* Yokohama, Japan.
IUCN AND WRI 2014. A Guide to the Restoration Opportunities Assessment Methodology (ROAM): Assessing forest landscape restoration opportunities at the national or subnational level. *Working Paper (Road-test edition).* Gland, Switzerland: INCN.
IUSS WORKING GROUP WRB 2014. World Reference Base for Soil Resources 2014. *World Soil Resources Reports No. 106.* Rome: FAO.
IVES, A. R. & CARPENTER, S. R. 2007. Stability and diversity of ecosystems. *science,* 317**,** 58-62.
IWATA, T., NAKANO, S. & INOUE, M. 2003. Impacts of past riparian deforestation on stream communities in a tropical rain forest in Borneo. *Ecological Applications,* 13**,** 461-473.
JENKINS, C. N., PIMM, S. L. & JOPPA, L. N. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences,* 110**,** E2602-E2610.
JENNY, H. 1941. *Factors of soil formation: A System of Quantitative Pedology* New York, McGraw-Hill.
JEPSEN, M. R. 2006. Above-ground carbon stocks in tropical fallows, Sarawak, Malaysia. *Forest ecology and management,* 225**,** 287-295.
JOHNSON, C. M., VIEIRA, I. C., ZARIN, D. J., FRIZANO, J. & JOHNSON, A. H. 2001. Carbon and nutrient storage in primary and secondary forests in eastern Amazonia. *Forest Ecology and Management,* 147**,** 245-252.
JUNQUEIRA, A. B., SHEPARD, G. H. & CLEMENT, C. R. 2010. Secondary forests on anthropogenic soils in Brazilian Amazonia conserve agrobiodiversity. *Biodiversity and Conservation,* 19**,** 1933-1961.
KANOWSKI, J., CATTERALL, C., WARDELL-JOHNSON, G., PROCTOR, H. & REIS, T. 2003. Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. *Forest Ecology and Management,* 183**,** 265-280.

KANOWSKI, J. & CATTERALL, C. P. 2010. Carbon stocks in above‐ground biomass of monoculture plantations, mixed species plantations and environmental restoration plantings in north‐east Australia. *Ecological Management & Restoration,* 11**,** 119-126.

KATENDE, A. B., BIRNIE, A. & TENGNAS, B. 1995. Useful trees and shrubs for Uganda. Identification, propagation and management for agricultural and pastoral communities. *Nairobi: Regional Soil Conservation Unit* 9966**,** 22.

KEEFE, K., SCHULZE, M., PINHEIRO, C., ZWEEDE, J. & ZARIN, D. 2009. Enrichment planting as a silvicultural option in the eastern Amazon: case study of Fazenda Cauaxi. *Forest Ecology and Management,* 258**,** 1950-1959.

KENNARD, D. K. 2002. Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. *Journal of Tropical Ecology,* 18**,** 53-66.

KENZO, T., ICHIE, T., HATTORI, D., KENDAWANG, J. J., SAKURAI, K. & NINOMIYA, I. 2010. Changes in above- and belowground biomass in early successional tropical secondary forests after shifting cultivation in Sarawak, Malaysia. *Forest Ecology and Management,* 260**,** 875-882.

KHALID, H., ZIN, Z. & ANDERSON, J. 1999. Quantification of oil palm biomass and nutrient value in a mature plantation. I. Above-ground biomass. *Journal of Oil Palm Research,* 11**,** 23-32.

KHO, L. K., MALHI, Y. & TAN, S. K. S. 2013. Annual budget and seasonal variation of aboveground and belowground net primary productivity in a lowland dipterocarp forest in Borneo. *Journal of Geophysical Research: Biogeosciences,* 118**,** 1282-1296.

KIYONO, Y. 2005. Patterns of slash-and-burn land use and their effects on forest succession: Swidden-land forests in Borneo [Indonesia]. *Bulletin of the Forestry and Forest Products Research Institute,* 4.

KOH, L. P., MIETTINEN, J., LIEW, S. C. & GHAZOUL, J. 2011. Remotely sensed evidence of tropical peatland conversion to oil palm. *Proceedings of the National Academy of Sciences,* 108**,** 5127-5132.

KOH, L. P. & WILCOVE, D. S. 2008. Is oil palm agriculture really destroying tropical biodiversity? *Conservation letters,* 1**,** 60-64.

KOHYAMA, T. 1986. Tree size structure of stands and each species in primary warm-temperate rain forests of southern Japan. *The botanical magazine= Shokubutsu-gaku-zasshi,* 99**,** 267-279.

KOHYAMA, T., HOTTA, M., OGINO, K., SYAHBUDDIN & MUKHTAR, E. 1989. Structure and dynamics of forest stands in Gunung Gadut, West Sumatra. *Diversity and Plant-Animal Interaction in Tropical Equatorial Forest: Report of the 1987-1988 Sumatra Research, Occasional Papers,* 16**,** 33-47.

KUARAKSA, C. & ELLIOTT, S. 2013. The Use of Asian Ficus Species for Restoring Tropical Forest Ecosystems. *Restoration Ecology,* 21**,** 86-95.

KUMAR, B. M. & NAIR, P. R. 2011. *Carbon sequestration potential of agroforestry systems: opportunities and challenges*, Springer Science & Business Media.

KÜRSTEN, E. & BURSCHEL, P. 1993. CO2-mitigation by agroforestry. *Water, Air, and Soil Pollution,* 70**,** 533-544.

KUSIN, F. M., AKHIR, N. I. M., MOHAMAT-YUSUFF, F. & AWANG, M. 2016. Nitrous oxide emission from nitrogen fertiliser application in oil palm plantation of different stages. *International Journal of Global Warming,* 9**,** 529-541.

LAESTADIUS, L., BUCKINGHAM, K., S., M. & SAINT-LAURENT, C. 2015. Before Bonn and beyond: the history and future of forest landscape restoration. *Unasylva,* 245**,** 11-18.

LAL, R. 2005. Forest soils and carbon sequestration. *Forest Ecology and Management,* 220**,** 242-258.

LAL, R. 2008. Carbon sequestration. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 363**,** 815-830.

LAMB, D. 2010. *Regreening the bare hills: tropical forest restoration in the Asia-Pacific region*, Springer.

LAMB, D., ERSKINE, P. & PARROTTA, J. 2005. Restoration of degraded tropical forest landscapes. *Science,* 310**,** 1628-32.

LANDE, R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. *The American Naturalist,* 142**,** 911-927.

LASCO, R. D., MACDICKEN, K. G., PULHIN, F. B., GUILLERMO, I. Q., SALES, R. F. & CRUZ, R. V. O. 2006. Carbon stocks assessment of a selectively logged dipterocarp forest and wood processing mill in the Philippines. *Journal of Tropical Forest Science,* 18**,** 212-221.

LAURANCE, W. F., CAMARGO, J. L. C., LUIZÃO, R. C. C., LAURANCE, S. G., PIMM, S. L., BRUNA, E. M., STOUFFER, P. C., BRUCE WILLIAMSON, G., BENÍTEZ-MALVIDO, J., VASCONCELOS, H. L., VAN HOUTAN, K. S., ZARTMAN, C. E., BOYLE, S. A., DIDHAM, R. K., ANDRADE, A. & LOVEJOY, T. E. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation,* 144**,** 56-67.

LAURANCE, W. F., CAROLINA USECHE, D., RENDEIRO, J., KALKA, M., BRADSHAW, C. J. A., SLOAN, S. P., LAURANCE, S. G., CAMPBELL, M., ABERNETHY, K., ALVAREZ, P., ARROYO-RODRIGUEZ, V., ASHTON, P., BENITEZ-MALVIDO, J., BLOM, A., BOBO, K. S., CANNON, C. H., CAO, M., CARROLL, R., CHAPMAN, C., COATES, R., CORDS, M., DANIELSEN, F., DE DIJN, B., DINERSTEIN, E., DONNELLY, M. A., EDWARDS, D., EDWARDS, F., FARWIG, N., FASHING, P., FORGET, P.-M., FOSTER, M., GALE, G., HARRIS, D., HARRISON, R., HART, J., KARPANTY, S., JOHN KRESS, W., KRISHNASWAMY, J., LOGSDON, W., LOVETT, J., MAGNUSSON, W., MAISELS, F., MARSHALL, A. R., MCCLEARN, D., MUDAPPA, D., NIELSEN, M. R., PEARSON, R., PITMAN, N., VAN DER PLOEG, J., PLUMPTRE, A., POULSEN, J., QUESADA, M., RAINEY, H., ROBINSON, D., ROETGERS, C., ROVERO, F., SCATENA, F., SCHULZE, C., SHEIL, D., STRUHSAKER, T., TERBORGH, J., THOMAS, D., TIMM, R., NICOLAS URBINA-CARDONA, J., VASUDEVAN, K., JOSEPH WRIGHT, S., CARLOS ARIAS-G, J., ARROYO, L., ASHTON, M., AUZEL, P., BABAASA, D., BABWETEERA, F., BAKER, P., BANKI, O., BASS, M., BILA-ISIA, I., BLAKE, S., BROCKELMAN, W., BROKAW, N., BRUHL, C. A., BUNYAVEJCHEWIN, S., CHAO, J.-T., CHAVE, J., CHELLAM, R., CLARK, C. J., CLAVIJO, J., CONGDON, R., CORLETT, R., DATTARAJA, H. S., DAVE, C., DAVIES, G., DE MELLO BEISIEGEL, B., DE NAZARE PAES DA SILVA, R., DI FIORE, A., DIESMOS, A., DIRZO, R., DORAN-SHEEHY, D., EATON, M., EMMONS, L., ESTRADA, A., et al. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature,* 489**,** 290-294.

LAURANCE, W. F., FEARNSIDE, P. M., LAURANCE, S. G., DELAMONICA, P., LOVEJOY, T. E., RANKIN-DE MERONA, J. M., CHAMBERS, J. Q. & GASCON, C. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management,* 118**,** 127-138.

LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M. & LAURANCE, S. G. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology,* 79**,** 2032-2040.

LAURANCE, W. F., LOVEJOY, T. E., VASCONCELOS, H. L., BRUNA, E. M., DIDHAM, R. K., STOUFFER, P. C., GASCON, C., BIERREGAARD, R. O., LAURANCE, S. G. & SAMPAIO, E. 2002. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. *Conservation Biology,* 16**,** 605-618.

LAVELLE, P., DECAËNS, T., AUBERT, M., BAROT, S., BLOUIN, M., BUREAU, F., MARGERIE, P., MORA, P. & ROSSI, J. P. 2006. Soil invertebrates and ecosystem services. *European Journal of Soil Biology,* 42, Supplement 1**,** S3-S15.

LAWES, M. & CHAPMAN, C. 2006. Does the herb Acanthus pubescens and/or elephants suppress tree regeneration in disturbed Afrotropical forest? *Forest ecology and management,* 221**,** 278-284.

LAWRENCE, D. 2005. Biomass accumulation after 10-200 years of shifting cultivation in Bornean rain forest. *Ecology,* 86**,** 26-33.

LE QUÉRÉ, C., MORIARTY, R., ANDREW, R. M., CANADELL, J. G., SITCH, S., KORSBAKKEN, J. I., FRIEDLINGSTEIN, P., PETERS, G. P., ANDRES, R. J. & BODEN, T. 2015. Global carbon budget 2015. *Earth System Science Data,* 7**,** 349-396.

LE QUÉRÉ, C., PETERS, G., ANDRES, R., ANDREW, R., BODEN, T., CIAIS, P., FRIEDLINGSTEIN, P., HOUGHTON, R., MARLAND, G. & MORIARTY, R. 2013. Global carbon budget 2013. *Earth System Science Data Discussions,* 6**,** 689-760.

LE QUERE, C., RAUPACH, M. R., CANADELL, J. G., MARLAND, G. & ET AL. 2009. Trends in the sources and sinks of carbon dioxide. *Nature Geosci,* 2**,** 831-836.

LEBLANC, S. G., CHEN, J. M., FERNANDES, R., DEERING, D. W. & CONLEY, A. 2005. Methodology comparison for canopy structure parameters extraction from digital hemispherical photography in boreal forests. *Agricultural and Forest Meteorology,* 129**,** 187-207.

LEBRIJA‐TREJOS, E., BONGERS, F., PÉREZ‐GARCÍA, E. A. & MEAVE, J. A. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica,* 40**,** 422-431.

LEE, H., DAVIES, S., LAFRANKIE, J., TAN, S., YAMAKURA, T., ITOH, A., OHKUBO, T. & ASHTON, P. 2002. Floristic and structural diversity of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. *Journal of Tropical Forest Science,* 14**,** 379-400.

LEITÃO, F. H., MARQUES, M. & CECCON, E. 2010. Young restored forests increase seedling recruitment in abandoned pastures in the Southern Atlantic rainforest. *Revista de Biología Tropical,* 58**,** 1271-1282.

LEPŠ, J. Š., PETR. 2003. *Multivariate analysis of ecological data using CANOCO,* New York, Cambridge University Press.

LETCHER, S. G. & CHAZDON, R. L. 2009. Rapid Recovery of Biomass, Species Richness, and Species Composition in a Forest Chronosequence in Northeastern Costa Rica. *Biotropica,* 41**,** 608-617.

LEVILLAIN, J., M'BOU, A. T., DELEPORTE, P., SAINT-ANDRÉ, L. & JOURDAN, C. 2011. Is the simple auger coring method reliable for below-ground standing biomass estimation in Eucalyptus forest plantations? *Annals of botany***,** mcr102.

LEWIS, S. L. 2006. Tropical forests and the changing earth system. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 361**,** 195-210.

LEWIS, S. L., LOPEZ-GONZALEZ, G., SONKE, B., AFFUM-BAFFOE, K., BAKER, T. R., OJO, L. O., PHILLIPS, O. L., REITSMA, J. M., WHITE, L., COMISKEY, J. A., DJUIKOUO, M. N., EWANGO, C. E. N., FELDPAUSCH, T. R., HAMILTON, A. C., GLOOR, M., HART, T., HLADIK, A., LLOYD, J., LOVETT, J. C., MAKANA, J. R., MALHI, Y., MBAGO, F. M., NDANGALASI, H. J., PEACOCK, J., PEH, K. S. H., SHEIL, D., SUNDERLAND, T., SWAINE, M. D., TAPLIN, J., TAYLOR, D., THOMAS, S. C., VOTERE, R. & WOLL, H. 2009. Increasing carbon storage in intact African tropical forests. *Nature,* 457**,** 1003-1006.

LEWIS, S. L., MALHI, Y. & PHILLIPS, O. L. 2004a. Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* 359**,** 437-462.

LEWIS, S. L., PHILLIPS, O. L., BAKER, T. R., LLOYD, J., MALHI, Y., ALMEIDA, S., HIGUCHI, N., LAURANCE, W. F., NEILL, D. A., SILVA, J. N. M., TERBORGH, J., LEZAMA, A. T., MARTINEZ, R. V., BROWN, S., CHAVE, J., KUEBLER, C., VARGAS, P. N. & VINCETI, B. 2004b. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences,* 359**,** 421-436.

LEWIS, S. L., SONKÉ, B., SUNDERLAND, T., BEGNE, S. K., LOPEZ-GONZALEZ, G., VAN DER HEIJDEN, G. M. F., PHILLIPS, O. L., AFFUM-BAFFOE, K., BAKER, T. R., BANIN, L., BASTIN, J.-F., BEECKMAN, H., BOECKX, P., BOGAERT, J., DE CANNIÈRE, C., CHEZEAUX, E., CLARK, C. J., COLLINS, M., DJAGBLETEY, G., DJUIKOUO, M. N. K., DROISSART, V., DOUCET, J.-L., EWANGO, C. E. N., FAUSET, S., FELDPAUSCH, T. R., FOLI, E. G., GILLET, J.-F., HAMILTON, A. C., HARRIS, D. J., HART, T. B., DE HAULLEVILLE, T., HLADIK, A., HUFKENS, K., HUYGENS, D., JEANMART, P., JEFFERY, K. J., KEARSLEY, E., LEAL, M. E., LLOYD, J., LOVETT, J. C., MAKANA, J.-R., MALHI, Y., MARSHALL, A. R., OJO, L., PEH, K. S.-H., PICKAVANCE, G., POULSEN, J. R., REITSMA, J. M., SHEIL, D., SIMO, M., STEPPE, K., TAEDOUMG, H. E., TALBOT, J., TAPLIN, J. R. D., TAYLOR, D., THOMAS, S. C., TOIRAMBE, B., VERBEECK, H., VLEMINCKX, J., WHITE, L. J. T., WILLCOCK, S., WOELL, H. & ZEMAGHO, L. 2013. Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 368.

LICHSTEIN, J. W., WIRTH, C., HORN, H. S. & PACALA, S. W. 2009. Biomass chronosequences of United States forests: implications for carbon storage and forest management. *Old-Growth Forests.* Springer.

LIU, Y., STANTURF, J. & GOODRICK, S. 2010. Trends in global wildfire potential in a changing climate. *Forest Ecology and Management,* 259**,** 685-697.

LONSDALE, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology,* 80**,** 1522-1536.

LOREAU, M., NAEEM, S., INCHAUSTI, P., BENGTSSON, J., GRIME, J., HECTOR, A., HOOPER, D., HUSTON, M., RAFFAELLI, D. & SCHMID, B. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *science,* 294**,** 804-808.

LOVE, A., BABU, S. & BABU, C. R. 2009. Management of Lantana, an invasive alien weed, in forest ecosystems of India. *Current Science,* 97**,** 1421-1429.

LUSIANA, B. & VAN NOORDWIJK, M. A. R., S. 2005. Carbon stocks in Nunukan, East Kalimantan: a spatial monitoring and modelling approach. . *Report from the carbon monitoring team of the Forest Resources Management for Carbon Sequestration (FORMACS)* Bogor, Indonesia: World Agroforestry Centre.

LUYSSAERT, S., INGLIMA, I., JUNG, M., RICHARDSON, A., REICHSTEIN, M., PAPALE, D., PIAO, S., SCHULZE, E. D., WINGATE, L. & MATTEUCCI, G. 2007. CO2 balance of boreal, temperate, and tropical forests derived from a global database. *Global change biology,* 13**,** 2509-2537.

MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography,* Princeton, Princeton University Press.

MACKEY, B., PRENTICE, I. C., STEFFEN, W., HOUSE, J. I., LINDENMAYER, D., KEITH, H. & BERRY, S. 2013. Untangling the confusion around land carbon science and climate change mitigation policy. *Nature climate change,* 3**,** 552-557.

MADEIRA, B. G., ESPÍRITO-SANTO, M. M., NETO, S. D. Â., NUNES, Y. R., AZOFEIFA, G. A. S., FERNANDES, G. W. & QUESADA, M. 2009. Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecology,* 201**,** 291-304.

MAES, W. H. & VERBIST, B. 2012. Increasing the sustainability of household cooking in developing countries: Policy implications. *Renewable and Sustainable Energy Reviews,* 16**,** 4204-4221.

MALAYSIAN PALM OIL BOARD. 2014. *Palm Oil Statistics* [Online]. Available: http://bepi.mpob.gov.my/index.php/statistics/area.html [Accessed 17/09/2015.
MALHI, Y. 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. *Journal of Ecology,* 100**,** 65-75.
MALHI, Y., BAKER, T. R., PHILLIPS, O. L., ALMEIDA, S., ALVAREZ, E., ARROYO, L., CHAVE, J., CZIMCZIK, C. I., FIORE, A. D. & HIGUCHI, N. 2004. The above‐ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology,* 10**,** 563-591.
MALHI, Y., BALDOCCHI, D. & JARVIS, P. 1999. The carbon balance of tropical, temperate and boreal forests. *Plant, Cell & Environment,* 22**,** 715-740.
MALHI, Y., DOUGHTY, C. & GALBRAITH, D. 2011. The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 366**,** 3225-3245.
MALHI, Y. & GRACE, J. 2000. Tropical forests and atmospheric carbon dioxide. *Trends in Ecology & Evolution,* 15**,** 332-337.
MALHI, Y., PEGORARO, E., NOBRE, A. D., PEREIRA, M. G. P., GRACE, J., CULF, A. D. & CLEMENT, R. 2002. Energy and water dynamics of a central Amazonian rain forest. *Journal of Geophysical Research: Atmospheres,* 107**,** 8061.
MALHI, Y., ROBERTS, J. T., BETTS, R. A., KILLEEN, T. J., LI, W. & NOBRE, C. A. 2008. Climate Change, Deforestation, and the Fate of the Amazon. *Science,* 319**,** 169-172.
MALHI, Y., WOOD, D., BAKER, T. R., WRIGHT, J., PHILLIPS, O. L., COCHRANE, T., MEIR, P., CHAVE, J., ALMEIDA, S. & ARROYO, L. 2006. The regional variation of aboveground live biomass in old‐growth Amazonian forests. *Global Change Biology,* 12**,** 1107-1138.
MALHI, Y. & WRIGHT, J. 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* 359**,** 311-329.
MARENGO, J. A., TOMASELLA, J., ALVES, L. M., SOARES, W. R. & RODRIGUEZ, D. A. 2011. The drought of 2010 in the context of historical droughts in the Amazon region. *Geophysical Research Letters,* 38**,** n/a-n/a.
MARIN-SPIOTTA, E., CUSACK, D. E., OSTERTAG, R. & SILVER, W. L. 2008. Trends in above and belowground carbon with forest regrowth after agricultural abandonment in the neotropics. *In:* MYSTER, R. W. (ed.) *Post - Agricultural Succession in the Neotropics.* New York: Springer.
MARIN-SPIOTTA, E., OSTERTAG, R. & SILVER, W. L. 2007. Long-term Patterns in Tropical Reforestation: Plant Community Composition and Aboveground Biomass Accumulation. *Ecological Applications,* 17**,** 828-839.
MARSH, C. W. & GREER, A. G. 1992. Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 335**,** 331-339.
MARTIN, P. A., NEWTON, A. C. & BULLOCK, J. M. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the Royal Society B-Biological Sciences,* 280.
MARTIN, P. A., NEWTON, A. C., PFEIFER, M., KHOO, M. & BULLOCK, J. M. 2015. Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis. *Forest Ecology and Management,* 356**,** 224-233.
MARTÍNEZ, L. & ZINCK, J. 2004. Temporal variation of soil compaction and deterioration of soil quality in pasture areas of Colombian Amazonia. *Soil and Tillage Research,* 75**,** 3-18.
MARTÍNEZ-GARZA, C., BONGERS, F. & POORTER, L. 2013. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *Forest Ecology and Management,* 303**,** 35-45.

MARTÍNEZ-GARZA, C., PENA, V., RICKER, M., CAMPOS, A. & HOWE, H. F. 2005. Restoring tropical biodiversity: leaf traits predict growth and survival of late-successional trees in early-successional environments. *Forest Ecology and Management,* 217**,** 365-379.

MARVIN, D. C. & ASNER, G. P. 2016. Spatially explicit analysis of field inventories for national forest carbon monitoring. *Carbon Balance and Management,* 11**,** 1-12.

MASSAD, T., CHAMBERS, J., ROLIM, S., JESUS, R. & DYER, L. 2011. Restoration of Pasture to Forest in Brazil's Mata Atlantica: The Roles of Herbivory, Seedling Defenses, and Plot Design in Reforestation. *Restoration Ecology,* 19**,** 257-267.

MAY, R. M. 2000. The dimensions of life on earth. *Nature and human society***,** 30-45.

MAYAUX, P., HOLMGREN, P., ACHARD, F., EVA, H., STIBIG, H. & BRANTHOMME, A. 2005. Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 360**,** 373-384.

MAZZEI, L., SIST, P., RUSCHEL, A., PUTZ, F. E., MARCO, P., PENA, W. & FERREIRA, J. E. R. 2010. Above-ground biomass dynamics after reduced-impact logging in the Eastern Amazon. *Forest Ecology and Management,* 259**,** 367-373.

MCNAMARA, S., TINH, D. V., ERSKINE, P. D., LAMB, D., YATES, D. & BROWN, S. 2006. Rehabilitating degraded forest land in central Vietnam with mixed native species plantings. *Forest Ecology and Management,* 233**,** 358-365.

MEA 2005. Ecosystems and human well-being : current state and trends. *In:* HASSAN, R., SCHOLES, R. & ASH, N. (eds.).

MEAD, D. J. 2005. Forests for energy and the role of planted trees. *BPTS,* 24**,** 407-421.

MEIR, P., COX, P. & GRACE, J. 2006. The influence of terrestrial ecosystems on climate. *Trends in Ecology & Evolution,* 21**,** 254-260.

MENDELSOHN, R. & BALICK, M. 1995. The value of undiscovered pharmaceuticals in tropical forests. *Economic Botany,* 49**,** 223-228.

MIETTINEN, J., HOOIJER, A., SHI, C., TOLLENAAR, D., VERNIMMEN, R., LIEW, S. C., MALINS, C. & PAGE, S. E. 2012. Extent of industrial plantations on Southeast Asian peatlands in 2010 with analysis of historical expansion and future projections. *GCB Bioenergy,* 4**,** 908-918.

MIETTINEN, J., SHI, C. & LIEW, S. C. 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology,* 17**,** 2261-2270.

MILES, L., TRUMPER, K., OSTI, M., MUNROE, R. & SANTAMARIA, C. 2012. REDD+ and the 2020 Aichi Biodiversity Targets: Promoting synergies in international forest conservation efforts. *Policy brief No. 5.* UN-REDD Programme.

MINNEMEYER, S., LAESTADIUS, L., SIZER, N., SAINT-LAURENT, C. & POTAPOV, P. V. 2011. Bonn Challenge: A World of Opportunity *Availible at:* http://www.forestlandscaperestoration.org/resource/bonn-challenge-world-opportunity. World Resource Institute.

MITCHARD, E. T., FELDPAUSCH, T. R., BRIENEN, R. J., LOPEZ‐GONZALEZ, G., MONTEAGUDO, A., BAKER, T. R., LEWIS, S. L., LLOYD, J., QUESADA, C. A. & GLOOR, M. 2014. Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. *Global Ecology and Biogeography*.

MITCHARD, E. T. A., SAATCHI, S. S., WHITE, L. J. T., ABERNETHY, K. A., JEFFERY, K. J., LEWIS, S. L., COLLINS, M., LEFSKY, M. A., LEAL, M. E., WOODHOUSE, I. H. & MEIR, P. 2012. Mapping tropical forest biomass with radar and spaceborne LiDAR in Lope National Park, Gabon: overcoming problems of high biomass and persistent cloud. *Biogeosciences,* 9**,** 179-191.

MOKANY, K., RAISON, R. & PROKUSHKIN, A. S. 2006. Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biology,* 12**,** 84-96.

MORA, C., TITTENSOR, D. P., ADL, S., SIMPSON, A. G. & WORM, B. 2011. How many species are there on Earth and in the ocean? *PLoS biology,* 9**,** e1001127.

MORA, F., MARTÍNEZ‐RAMOS, M., IBARRA‐MANRÍQUEZ, G., PÉREZ‐JIMÉNEZ, A., TRILLERAS, J. & BALVANERA, P. 2015. Testing chronosequences through dynamic approaches: time and site effects on tropical dry forest succession. *Biotropica,* 47**,** 38-48.

MOREL, A. C., FISHER, J. B. & MALHI, Y. 2012. Evaluating the potential to monitor aboveground biomass in forest and oil palm in Sabah, Malaysia, for 2000–2008 with Landsat ETM+ and ALOS-PALSAR. *International Journal of Remote Sensing,* 33**,** 3614-3639.

MOREL, A. C., SAATCHI, S. S., MALHI, Y., BERRY, N. J., BANIN, L., BURSLEM, D., NILUS, R. & ONG, R. C. 2011. Estimating aboveground biomass in forest and oil palm plantation in Sabah, Malaysian Borneo using ALOS PALSAR data. *Forest Ecology and Management,* 262**,** 1786-1798.

MOSER, G., LEUSCHNER, C., HERTEL, D., GRAEFE, S., SOETHE, N. & IOST, S. 2011. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology,* 17**,** 2211-2226.

MUGAGGA, F., KAKEMBO, V. & BUYINZA, M. 2012. Land use changes on the slopes of Mount Elgon and the implications for the occurrence of landslides. *CATENA,* 90**,** 39-46.

MURCIA, C., GUARIGUATA, M. R., ANDRADE, Á., ANDRADE, G. I., ARONSON, J., ESCOBAR, E. M., ETTER, A., MORENO, F. H., RAMÍREZ, W. & MONTES, E. 2015. Challenges and prospects for scaling‐up ecological restoration to meet international commitments: Colombia as a case study. *Conservation Letters*.

MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. B. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature,* 403**,** 853-858.

NAIR, P. R., KUMAR, B. M. & NAIR, D. V. 2009. Agroforestry as a strategy for carbon sequestration. *Journal of Plant Nutrition and Soil Science,* 172**,** 10-23.

NG, S., THAMBOO, S. & DE SOUZA, P. 1968. Nutrient contents of oil palms in Malaysa. II. Nutrients in vegetative tissues. *Malaysian Agricultural Jornal,* 46**,** 332-391.

NIIYAMA, K., KAJIMOTO, T., MATSUURA, Y., YAMASHITA, T., MATSUO, N., YASHIRO, Y., RIPIN, A., KASSIM, A. R. & NOOR, N. S. 2010. Estimation of root biomass based on excavation of individual root systems in a primary dipterocarp forest in Pasoh Forest Reserve, Peninsular Malaysia. *Journal of Tropical Ecology,* 26**,** 271-284.

NIÑO, M., MCLAREN, K. P., MEILBY, H., LÉVESQUE, M., WILSON, B. & MCDONALD, M. 2014. Long-term changes in above ground biomass after disturbance in a neotropical dry forest, Hellshire Hills, Jamaica. *Plant Ecology,* 215**,** 1081-1097.

NOGUEIRA LIMA, A., TEIXEIRA, L., COLARES CARNEIRO, V., DOS SANTOS, J. & HIGUCHI, N. 2007. Biomass stock and structural analysis of a secondary forest in Manaus (AM) region, ten years after clear cutting followed by fire. *Acta amazonica,* 37**,** 49-53.

NOVOTNY, V. & BASSET, Y. 2005. Host specificity of insect herbivores in tropical forests. *Proceedings of the Royal Society B: Biological Sciences,* 272**,** 1083-1090.

NUNEZ-CRUZ, A. & BONFIL, C. 2013. Initial establishment of three species of tropical dry forest in a degraded pasture: effects of adding mulch and compost. *Agrociencia,* 47**,** 609-620.

NUSSBAUM, R., ANDERSON, J. & SPENCER, T. 1995. Factors limiting the growth of indigenous tree seedlings planted on degraded rainforest soils in Sabah, Malaysia. *Forest Ecology and Management,* 74**,** 149-159.

OELBERMANN, M., VORONEY, R. P. & GORDON, A. M. 2004. Carbon sequestration in tropical and temperate agroforestry systems: a review with examples from Costa Rica and southern Canada. *Agriculture, ecosystems & environment,* 104**,** 359-377.

OESTREICHER, J. S., BENESSAIAH, K., RUIZ-JAEN, M. C., SLOAN, S., TURNER, K., PELLETIER, J., GUAY, B., CLARK, K. E., ROCHE, D. G., MEINERS, M. & POTVIN, C. 2009. Avoiding deforestation in Panamanian protected areas: An analysis of protection effectiveness and implications for reducing emissions from deforestation and forest degradation. *Global Environmental Change,* 19**,** 279-291.

OHTSUKA, T. 2001. Biomass Changes in Early Tropical Succession on a Large-scale Shifting Cultivation Area, Northeast Borneo Island. *Tropics,* 10**,** 529-537.

OKSANEN, J. F. B., GUILLAUME KINDT, ROELAND , LEGENDRE, P., MINCHIN, P. R., O'HARA, R. B. & SIMPSON, G. L. S., PETER M. STEVENS HENRY H. WAGNER, HELENE 2013. vegan: Community Ecology Package. R package version 2.0-10 ed. http://CRAN.R-project.org/package=vegan.

OLLERTON, J., WINFREE, R. & TARRANT, S. 2011. How many flowering plants are pollinated by animals? *Oikos,* 120**,** 321-326.

OMEJA, P., CHAPMAN, C., OBUA, J., LWANGA, J., JACOB, A. L., WANYAMA, F. & MUGENYI, R. 2011a. Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation in Kibale National Park, Uganda *Forest Ecology and Management,* 261**,** 703-709.

OMEJA, P., LWANGA, J., OBUA, J. & CHAPMAN, C. 2011b. Fire control as a simple means of promoting tropical forest restoration. *Tropical Conservation Science,* 4**,** 287-299.

ONRIZAL, K. C. M., M. HARTONO, R. 2009. Allometric biomass and carbon stock equations of planted Eucalyptus grandis in. *Research on Plantation Forests: challenges and Opportunities, .* Bogor, Indonesia.

ORIHUELA-BELMONTE, D., DE JONG, B., MENDOZA-VEGA, J., VAN DER WAL, J., PAZ-PELLAT, F., SOTO-PINTO, L. & FLAMENCO-SANDOVAL, A. 2013. Carbon stocks and accumulation rates in tropical secondary forests at the scale of community, landscape and forest type. *Agriculture, Ecosystems & Environment,* 171**,** 72-84.

ORTEGA-PIECK, A., LÓPEZ-BARRERA, F., RAMÍREZ-MARCIAL, N. & GARCÍA-FRANCO, J. G. 2011. Early seedling establishment of two tropical montane cloud forest tree species: The role of native and exotic grasses. *Forest Ecology and Management,* 261**,** 1336-1343.

OSMASTON, H. A. 1959. Forestry Working Plan for the Kibale and Itwara Forests. Entebbe, Uganda: Uganda Forest Department.

PAGE, S. E., SIEGERT, F., RIELEY, J. O., BOEHM, H.-D. V., JAYA, A. & LIMIN, S. 2002. The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature,* 420**,** 61-65.

PALACE, M., HURTT, G., KELLER, M. & FROLKING, S. 2012. *A review of above ground necromass in tropical forests*, INTECH Open Access Publisher.

PALM, C. A., WOOMER, P., ALEGRE, J., AREVALO, L., CASTILLA, C., CORDEIRO, D., FEIGL, B., HAIRIAH, K., KOTTO-SAME, J. & MENDES, A. 1999. *Carbon sequestration and trace gas emissions in slash-and-burn and alternative land-uses in the humid tropics*, ASB Coordination Office, ICRAF Nairobi, Kenya.

PAN, Y., BIRDSEY, R. A., FANG, J., HOUGHTON, R., KAUPPI, P. E., KURZ, W. A., PHILLIPS, O. L., SHVIDENKO, A., LEWIS, S. L. & CANADELL, J. G. 2011. A large and persistent carbon sink in the world's forests. *Science,* 333**,** 988-993.

PAOLI, G. D., CURRAN, L. M. & SLIK, J. 2008. Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia,* 155**,** 287-299.

PARKER, C., MITCHELL, A., & TRIVEDI, M., MARDAS, N. 2009. The Little REDD+ Book. Oxford, UK: Global Canopy Programme.

PARROTTA, J. A. & KNOWLES, O. H. 1999. Restoration of Tropical Moist Forests on Bauxite - Mined Lands in the Brazilian Amazon. *Restoration ecology,* 7**,** 103-116.

PAUL, J. R., RANDLE, A. M., CHAPMAN, C. A. & CHAPMAN, L. J. 2004. Arrested succession in logging gaps: is tree seedling growth and survival limiting? *African Journal of Ecology,* 42**,** 245-251.

PAUL, K. I., ROXBURGH, S. H., ENGLAND, J. R., DE LIGT, R., LARMOUR, J. S., BROOKSBANK, K., MURPHY, S., RITSON, P., HOBBS, T. & LEWIS, T. 2015. Improved models for estimating temporal changes in carbon sequestration in above-ground biomass of mixed-species environmental plantings. *Forest Ecology and Management,* 338**,** 208-218.

PEDRAZA, R. & WILLIAMS-LINERA, G. 2003. Evaluation of native tree species for the rehabilitation of deforested areas in a Mexican cloud forest. *New Forests,* 26**,** 83-99.

PEH, K. S. H., LEWIS, S. L. & LLOYD, J. 2011. Mechanisms of monodominance in diverse tropical tree-dominated systems. *Journal of Ecology,* 99**,** 891-898.

PEH, K. S. H., SODHI, N. S., DE JONG, J., SEKERCIOGLU, C. H., YAP, C. A. M. & LIM, S. L. H. 2006. Conservation value of degraded habitats for forest birds in southern Peninsular Malaysia. *Diversity and Distributions,* 12**,** 572-581.

PEÑA-CLAROS, M., FREDERICKSEN, T. S., ALARCÓN, A., BLATE, G. M., CHOQUE, U., LEAÑO, C., LICONA, J. C., MOSTACEDO, B., PARIONA, W., VILLEGAS, Z. & PUTZ, F. E. 2008. Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. *Forest Ecology and Management,* 256**,** 1458-1467.

PEÑA‐CLAROS, M. 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon1. *Biotropica,* 35**,** 450-461.

PEREIRA, S. R., LAURA, V. A. & SOUZA, A. L. 2013. Establishment of Fabaceae tree species in a tropical pasture: influence of seed size and weeding methods. *Restoration Ecology,* 21**,** 67-74.

PEREZ-HERNANDEZ, I., OCHOA-GAONA, S., VARGAS-SIMON, G., MENDOZA-CARRANZA, M. & ANTONIO GONZALEZ-VALDIVIA, N. 2011. Germination and survival of six native species in a tropical forest of Tabasco, Mexico. *Madera Y Bosques,* 17**,** 71-91.

PHELPS, J., WEBB, E. L. & AGRAWAL, A. 2010. Does REDD+ threaten to recentralize forest governance. *Science,* 328**,** 312-313.

PHILIPSON, C. D., DENT, D. H., O'BRIEN, M. J., CHAMAGNE, J., DZULKIFLI, D., NILUS, R., PHILIPS, S., REYNOLDS, G., SANER, P. & HECTOR, A. 2014. A trait‐based trade‐off between growth and mortality: evidence from 15 tropical tree species using size‐specific relative growth rates. *Ecology and evolution,* 4**,** 3675-3688.

PHILLIPS, O., BAKER, T., FELDPAUSCH, T. & BRIENEN, R. 2009a. *RAINFOR field manual for plot establishment and remeasurement* [Online]. http://www.rainfor.org/en/manuals.

PHILLIPS, O. L., ARAGÃO, L. E., LEWIS, S. L., FISHER, J. B., LLOYD, J., LÓPEZ-GONZÁLEZ, G., MALHI, Y., MONTEAGUDO, A., PEACOCK, J. & QUESADA, C. A. 2009b. Drought sensitivity of the Amazon rainforest. *Science,* 323**,** 1344-1347.

PHILLIPS, O. L. & GENTRY, A. H. 1994. Increasing turnover through time in tropical forests. *Science,* 263**,** 954-958.

PHILLIPS, O. L. & LEWIS, S. L. 2014. Evaluating the tropical forest carbon sink. *Global Change Biology,* 20**,** 2039-2041.

PHILLIPS, O. L., LEWIS, S. L., BAKER, T. R., CHAO, K. J. & HIGUCHI, N. 2008. The changing Amazon forest. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 363**,** 1819-1827.

PINARD, M. A. & PUTZ, F. E. 1994. Vine infestation of large remnant trees in logged forest in Sabah, Malaysia: Biomechanical facilitation in vine succession. *Journal of tropical forest science,* 6**,** 302-309.

PINARD, M. A. & PUTZ, F. E. 1996. Retaining forest biomass by reducing logging damage. *Biotropica,* 28**,** 278-295.

PINHEIRO, J., BATES, D. & R CORE TEAM 2016. nlme: Linear and Non-Linear Mixed Effects Models. 3.1-128 ed.

PIOTTO, D. 2011. *Spatial dynamics of forest recovery after swidden cultivation in the Atlantic forest of southern Bahia, Brazil.* Doctor of Philosophy, Yale University.

PISTORIUS, T. 2012. From RED to REDD+: the evolution of a forest-based mitigation approach for developing countries. *Current Opinion in Environmental Sustainability,* 4**,** 638-645.

PLATH, M., MODY, K., POTVIN, C. & DORN, S. 2011. Establishment of native tropical timber trees in monoculture and mixed-species plantations: small-scale effects on tree performance and insect herbivory. *Forest Ecology and Management,* 261**,** 741-750.

POORTER, L., BONGERS, F., AIDE, T. M., ZAMBRANO, A. M. A., BALVANERA, P., BECKNELL, J. M., BOUKILI, V., BRANCALION, P. H., BROADBENT, E. N. & CHAZDON, R. L. 2016. Biomass resilience of Neotropical secondary forests. *Nature,* 530**,** 211-214.

POWERS, J. S., BECKNELL, J. M., IRVING, J. & PÈREZ-AVILES, D. 2009. Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. *Forest Ecology and Management,* 258**,** 959-970.

PREECE, N. D., CROWLEY, G. M., LAWES, M. J. & VAN OOSTERZEE, P. 2012. Comparing above-ground biomass among forest types in the Wet Tropics: Small stems and plantation types matter in carbon accounting. *Forest Ecology and Management,* 264**,** 228-237.

PREECE, N. D., LAWES, M. J., ROSSMAN, A. K., CURRAN, T. J. & VAN OOSTERZEE, P. 2015. Modelling the growth of young rainforest trees for biomass estimates and carbon sequestration accounting. *Forest Ecology and Management,* 351**,** 57-66.

PROCTOR, S., MCCLEAN, C. J. & HILL, J. K. 2011. Protected areas of Borneo fail to protect forest landscapes with high habitat connectivity. *Biodiversity and Conservation,* 20**,** 2693-2704.

PULLIN, A. S. & STEWART, G. B. 2006. Guidelines for systematic review in conservation and environmental management. *Conservation biology,* 20**,** 1647-1656.

PUTZ, F. E. & REDFORD, K. H. 2010. The Importance of Defining 'Forest': Tropical Forest Degradation, Deforestation, Long-term Phase Shifts, and Further Transitions. *Biotropica,* 42**,** 10-20.

PUTZ, F. E., REDFORD, K. H., ROBINSON, J. G., FIMBEL, R. & BLATE, G. M. 2000. Biodiversity conservation in the context of tropical forest management.

PUTZ, F. E., SIST, P., FREDERICKSEN, T. & DYKSTRA, D. 2008. Reduced-impact logging: Challenges and opportunities. *Forest Ecology and Management,* 256**,** 1427-1433.

PUTZ, F. E., ZUIDEMA, P. A., SYNNOTT, T., PEÑA‐CLAROS, M., PINARD, M. A., SHEIL, D., VANCLAY, J. K., SIST, P., GOURLET‐FLEURY, S. & GRISCOM, B. 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters,* 5**,** 296-303.

QUESADA, C., LLOYD, J., SCHWARZ, M., PATIÃ±O, S., BAKER, T., CZIMCZIK, C., FYLLAS, N., MARTINELLI, L., NARDOTO, G. & SCHMERLER, J. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences,* 7**,** 3923-3992.

QUESADA, C. A., PHILLIPS, O. L., SCHWARZ, M., CZIMCZIK, C. I., BAKER, T. R., PATIÃ±O, S., FYLLAS, N. M., HODNETT, M. G., HERRERA, R., ALMEIDA, S., ALVAREZ DÃ¡VILA, E., ARNETH, A., ARROYO, L., CHAO, K. J., DEZZEO, N., ERWIN, T., DI FIORE, A., HIGUCHI, N., HONORIO CORONADO, E., JIMENEZ, E. M., KILLEEN, T., LEZAMA, A. T., LLOYD, G., LÃ³PEZ-GONZÃ¡LEZ, G., LUIZÃ£O, F. J., MALHI, Y., MONTEAGUDO, A., NEILL, D. A., NÃºÃ±EZ VARGAS, P., PAIVA, R., PEACOCK, J., PEÃ±UELA, M. C., PEÃ±A CRUZ, A., PITMAN, N., PRIANTE FILHO, N., PRIETO, A., RAMÃ-REZ, H., RUDAS, A., SALOMÃ£O, R., SANTOS, A. J. B., SCHMERLER, J., SILVA, N., SILVEIRA, M.,

VÃ¡SQUEZ, R., VIEIRA, I., TERBORGH, J. & LLOYD, J. 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate.
R CORE TEAM 2013. R: A language and environment for statistical computing. Vienna, Austria. : R Foundation for Statistical Computing, http://www.R-project.org/.
RAHARIMALALA, O., BUTTLER, A., SCHLAEPFER, R. & GOBAT, J. M. 2012. Quantifying biomass of secondary forest after slash-and-burn cultivation in central menabe, Madagascar. *Journal of Tropical Forest Science,* 24**,** 474-489.
RAINFOR. 2009. *Rainfor Amazon Plot Inventory Network* http://www.rainfor.org/en [Online]. [accessed September 2015].
RAMAN, T., MUDAPPA, D. & KAPOOR, V. 2009. Restoring Rainforest Fragments: Survival of Mixed‐Native Species Seedlings under Contrasting Site Conditions in the Western Ghats, India. *Restoration Ecology,* 17**,** 137-147.
REES, M., CONDIT, R., CRAWLEY, M., PACALA, S. & TILMAN, D. 2001. Long-term studies of vegetation dynamics. *Science,* 293**,** 650-655.
REYNOLDS, G., PAYNE, J., SINUN, W., MOSIGIL, G. & WALSH, R. P. 2011. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum Valley region. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 366**,** 3168-3176.
RIST, L., SHANLEY, P., SUNDERLAND, T., SHEIL, D., NDOYE, O., LISWANTI, N. & TIEGUHONG, J. 2012. The impacts of selective logging on non-timber forest products of livelihood importance. *Forest Ecology and Management,* 268**,** 57-69.
RISWAN, S. 1985. The estimation of temporal processes in tropical rain forest: A study of primary mixed dipterocarp forest in Indonesia. *Journal of tropical ecology,* 1**,** 171.
ROGELJ, J., DEN ELZEN, M., HÖHNE, N., FRANSEN, T., FEKETE, H., WINKLER, H., SCHAEFFER, R., SHA, F., RIAHI, K. & MEINSHAUSEN, M. 2016. Paris Agreement climate proposals need a boost to keep warming well below 2 °C. *Nature,* 534**,** 631-639.
ROMÁN‐DAÑOBEYTIA, F. J., LEVY‐TACHER, S. I., ARONSON, J., RODRIGUES, R. R. & CASTELLANOS‐ALBORES, J. 2012. Testing the performance of fourteen native tropical tree species in two abandoned pastures of the Lacandon rainforest region of Chiapas, Mexico. *Restoration Ecology,* 20**,** 378-386.
RUDEL, T. K., DEFRIES, R., ASNER, G. P. & LAURANCE, W. F. 2009. Changing Drivers of Deforestation and New Opportunities for Conservation. *Conservation Biology,* 23**,** 1396-1405.
RUIZ, J., FANDIÑO, M. C. & CHAZDON, R. L. 2005. Vegetation Structure, Composition, and Species Richness Across a 56-year Chronosequence of Dry Tropical Forest on Providencia Island, Colombia1. *Biotropica,* 37**,** 520-530.
RUIZ-JAEN, M. C. & POTVIN, C. 2010. Tree Diversity Explains Variation in Ecosystem Function in a Neotropical Forest in Panama. *Biotropica,* 42**,** 638-646.
SAATCHI, S. S., HARRIS, N. L., BROWN, S., LEFSKY, M., MITCHARD, E. T., SALAS, W., ZUTTA, B. R., BUERMANN, W., LEWIS, S. L. & HAGEN, S. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences,* 108**,** 9899-9904.
SAATCHI, S. S., HOUGHTON, R. A., DOS SANTOS ALVALÁ, R. C., SOARES, J. V. & YU, Y. 2007. Distribution of aboveground live biomass in the Amazon basin. *Global Change Biology,* 13**,** 816-837.
SAHA, D. & SUNDRIYAL, R. C. 2012. Utilization of non-timber forest products in humid tropics: Implications for management and livelihood. *Forest Policy and Economics,* 14**,** 28-40.

SAINT-ANDRÉ, L., M'BOU, A. T., MABIALA, A., MOUVONDY, W., JOURDAN, C., ROUPSARD, O., DELEPORTE, P., HAMEL, O. & NOUVELLON, Y. 2005. Age-related equations for above-and below-ground biomass of a Eucalyptus hybrid in Congo. *Forest ecology and management,* 205**,** 199-214.

SALDARRIAGA, J. G., WEST, D. C., THARP, M. L. & UHL, C. 1988. Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela *Journal of Ecology,* 76**,** 938-958.

SALIMON, C. I. & BROWN, I. F. 2000. Secondary forests in western Amazonia: Significant sinks for carbon released from deforestation? *Interciencia,* 25**,** 198-202.

SAMPAIO, A. B., HOLL, K. D. & SCARIOT, A. 2007. Does restoration enhance regeneration of seasonal deciduous forests in pastures in central Brazil? *Restoration Ecology,* 15**,** 462-471.

SANER, P., LOH, Y. Y., ONG, R. C. & HECTOR, A. 2012. Carbon stocks and fluxes in tropical lowland dipterocarp rainforests in Sabah, Malaysian Borneo. *PloS one,* 7**,** e29642.

SANG, P. M., LAMB, D., BONNER, M. & SCHMIDT, S. 2013. Carbon sequestration and soil fertility of tropical tree plantations and secondary forest established on degraded land. *Plant and soil,* 362**,** 187-200.

SANQUETTA, C. R., ELLICONETTO, S., DALLA CORTE, A. P., RODRIGUES, A., LOURENÇO, E., BEHLIN, A. & SANQUETTA, M. N. I. 2015. Quantifying biomass and carbon stocks in oil palm (Elaeis guineensis Jacq.) in Northeastern Brazil. *African Journal of Agricultural Research,* 10**,** 4067-4075.

SANSEVERO, J. B. B., PRIETO, P. V., DE MORAES, L. F. D. & RODRIGUES, P. J. P. 2011. Natural regeneration in plantations of native trees in lowland Brazilian Atlantic Forest: community structure, diversity, and dispersal syndromes. *Restoration Ecology,* 19**,** 379-389.

SASAKI, N., ASNER, G. P., KNORR, W., DURST, P. B., PRIYADI, H. R. & PUTZ, F. E. 2011. Approaches to classifying and restoring degraded tropical forests for the anticipated REDD plus climate change mitigation mechanism. *Iforest-Biogeosciences and Forestry,* 4**,** 1-6.

SCHEFFERS, B. R., JOPPA, L. N., PIMM, S. L. & LAURANCE, W. F. 2012. What we know and don't know about Earth's missing biodiversity. *Trends in Ecology & Evolution,* 27**,** 501-510.

SCHROTH, G., D'ANGELO, S. A., TEIXEIRA, W. G., HAAG, D. & LIEBEREI, R. 2002. Conversion of secondary forest into agroforestry and monoculture plantations in Amazonia: consequences for biomass, litter and soil carbon stocks after 7 years. *Forest Ecology and Management,* 163**,** 131-150.

SCHWARTZ, M. W., BRIGHAM, C. A., HOEKSEMA, J. D., LYONS, K. G., MILLS, M. H. & VAN MANTGEM, P. J. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia,* 122**,** 297-305.

SHACKLETON, C. M. & PANDEY, A. K. 2014. Positioning non-timber forest products on the development agenda. *Forest Policy and Economics,* 38**,** 1-7.

SHEIL, D. & MAY, R. M. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology,* 84**,** 91-100.

SHIRIMA, D. D., MUNISHI, P. K. T., LEWIS, S. L., BURGESS, N. D., MARSHALL, A. R., BALMFORD, A., SWETNAM, R. D. & ZAHABU, E. M. 2011. Carbon storage, structure and composition of miombo woodlands in Tanzania's Eastern Arc Mountains. *African Journal of Ecology,* 49**,** 332-342.

SHONO, K., CADAWENG, E. A. & DURST, P. B. 2007a. Application of assisted natural regeneration to restore degraded tropical forestlands. *Restoration Ecology,* 15**,** 620-626.

SHONO, K., DAVIES, S. & CHUA, Y. 2007b. Performance of 45 native tree species on degraded lands in Singapore. *Journal of Tropical Forest Science,* 19**,** 25.

SHONO, K., DAVIES, S. J. & KHENG, C. Y. 2006. Regeneration of native plant species in restored forests on degraded lands in Singapore. *Forest Ecology and Management,* 237**,** 574-582.

SIERRA, C., DEL VALLE, J. & RESTREPO, H. 2012. Total carbon accumulation in a tropical forest landscape. *Carbon Balance and Management,* 7**,** 12-12.

SLIK, J. W. F., AIBA, S.-I., BREARLEY, F. Q., CANNON, C. H., FORSHED, O., KITAYAMA, K., NAGAMASU, H., NILUS, R., PAYNE, J., PAOLI, G., POULSEN, A. D., RAES, N., SHEIL, D., SIDIYASA, K., SUZUKI, E. & VAN VALKENBURG, J. L. C. H. 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography,* 19**,** 50-60.

SLIK, J. W. F., ARROYO-RODRÍGUEZ, V., AIBA, S.-I., ALVAREZ-LOAYZA, P., ALVES, L. F., ASHTON, P., BALVANERA, P., BASTIAN, M. L., BELLINGHAM, P. J., VAN DEN BERG, E., BERNACCI, L., DA CONCEIÇÃO BISPO, P., BLANC, L., BÖHNING-GAESE, K., BOECKX, P., BONGERS, F., BOYLE, B., BRADFORD, M., BREARLEY, F. Q., BREUER-NDOUNDOU HOCKEMBA, M., BUNYAVEJCHEWIN, S., CALDERADO LEAL MATOS, D., CASTILLO-SANTIAGO, M., CATHARINO, E. L. M., CHAI, S.-L., CHEN, Y., COLWELL, R. K., CHAZDON, R. L., CLARK, C., CLARK, D. B., CLARK, D. A., CULMSEE, H., DAMAS, K., DATTARAJA, H. S., DAUBY, G., DAVIDAR, P., DEWALT, S. J., DOUCET, J.-L., DUQUE, A., DURIGAN, G., EICHHORN, K. A. O., EISENLOHR, P. V., ELER, E., EWANGO, C., FARWIG, N., FEELEY, K. J., FERREIRA, L., FIELD, R., DE OLIVEIRA FILHO, A. T., FLETCHER, C., FORSHED, O., FRANCO, G., FREDRIKSSON, G., GILLESPIE, T., GILLET, J.-F., AMARNATH, G., GRIFFITH, D. M., GROGAN, J., GUNATILLEKE, N., HARRIS, D., HARRISON, R., HECTOR, A., HOMEIER, J., IMAI, N., ITOH, A., JANSEN, P. A., JOLY, C. A., DE JONG, B. H. J., KARTAWINATA, K., KEARSLEY, E., KELLY, D. L., KENFACK, D., KESSLER, M., KITAYAMA, K., KOOYMAN, R., LARNEY, E., LAUMONIER, Y., LAURANCE, S., LAURANCE, W. F., LAWES, M. J., AMARAL, I. L. D., LETCHER, S. G., LINDSELL, J., LU, X., MANSOR, A., MARJOKORPI, A., MARTIN, E. H., MEILBY, H., MELO, F. P. L., METCALFE, D. J., MEDJIBE, V. P., METZGER, J. P., MILLET, J., MOHANDASS, D., MONTERO, J. C., DE MORISSON VALERIANO, M., MUGERWA, B., NAGAMASU, H., NILUS, R., OCHOA-GAONA, S., et al. 2015. An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences,* 112**,** 7472-7477.

SNEDAKER, S. C. 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala.

STAPE, J. L., BINKLEY, D., RYAN, M. G., FONSECA, S., LOOS, R. A., TAKAHASHI, E. N., SILVA, C. R., SILVA, S. R., HAKAMADA, R. E. & FERREIRA, J. M. D. A. 2010. The Brazil Eucalyptus Potential Productivity Project: Influence of water, nutrients and stand uniformity on wood production. *Forest Ecology and Management,* 259**,** 1684-1694.

STEININGER, M. K. 2000. Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. *Journal of Tropical Ecology,* 16**,** 689-708.

STIBIG, H. J., ACHARD, F., CARBONI, S., RASI, R. & MIETTINEN, J. 2014. Change in tropical forest cover of Southeast Asia from 1990 to 2010. *Biogeosciences,* 11**,** 247-258.

STRUHSAKER, T. T. 1997. *Ecology of an African Rainforest: Logging in Kibale and the Conflict between Conservation and Exploitation,* Gainsville, Florida, University Press of Florida.

SUDING, K., HIGGS, E., PALMER, M., CALLICOTT, J. B., ANDERSON, C. B., BAKER, M., GUTRICH, J. J., HONDULA, K. L., LAFEVOR, M. C., LARSON, B. M. H., RANDALL, A., RUHL, J. B. & SCHWARTZ, K. Z. S. 2015. Committing to ecological restoration. *Science,* 348**,** 638-640.

SZOTT, L. T., PALM, C. A. & DAVEY, C. 1994. Biomass and litter accumulation under managed and natural tropical fallows. *Forest Ecology and Management,* 67**,** 177-190.

TALBOT, J., LEWIS, S. L., LOPEZ-GONZALEZ, G., BRIENEN, R. J. W., MONTEAGUDO, A., BAKER, T. R., FELDPAUSCH, T. R., MALHI, Y., VANDERWEL, M., ARAUJO MURAKAMI, A., ARROYO, L. P., CHAO, K.-J., ERWIN, T., VAN DER HEIJDEN, G., KEELING, H., KILLEEN, T., NEILL, D., NÚÑEZ VARGAS, P., PARADA GUTIERREZ, G. A., PITMAN, N., QUESADA, C. A., SILVEIRA, M., STROPP, J. & PHILLIPS, O. L. 2014. Methods to estimate aboveground wood productivity from long-term forest inventory plots. *Forest Ecology and Management,* 320**,** 30-38.

TANGKI, H. & CHAPPELL, N. A. 2008. Biomass variation across selectively logged forest within a 225-km 2 region of Borneo and its prediction by Landsat TM. *Forest Ecology and Management,* 256**,** 1960-1970.

TER STEEGE, H., PITMAN, N., SABATIER, D., CASTELLANOS, H., VAN DER HOUT, P., DALY, D. C., SILVEIRA, M., PHILLIPS, O., VASQUEZ, R. & VAN ANDEL, T. 2003. A spatial model of tree α-diversity and tree density for the Amazon. *Biodiversity & Conservation,* 12**,** 2255-2277.

TER STEEGE, H., PITMAN, N. C. A., PHILLIPS, O. L., CHAVE, J., SABATIER, D., DUQUE, A., MOLINO, J.-F., PREVOST, M.-F., SPICHIGER, R., CASTELLANOS, H., VON HILDEBRAND, P. & VASQUEZ, R. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature,* 443**,** 444-447.

TERBORGH, J., LOPEZ, L., NUÑEZ, P., RAO, M., SHAHABUDDIN, G., ORIHUELA, G., RIVEROS, M., ASCANIO, R., ADLER, G. H., LAMBERT, T. D. & BALBAS, L. 2001. Ecological Meltdown in Predator-Free Forest Fragments. *Science,* 294**,** 1923-1926.

THE BONN CHALLENGE. 2016. http://www.bonnchallenge.org/ [Online]. [accessed July 2015]. Available: http://www.bonnchallenge.org/ [Accessed July 2016.

THOMAS, S. C. & MARTIN, A. R. 2012. Carbon content of tree tissues: a synthesis. *Forests,* 3**,** 332-352.

THURNER, M., BEER, C., SANTORO, M., CARVALHAIS, N., WUTZLER, T., SCHEPASCHENKO, D., SHVIDENKO, A., KOMPTER, E., AHRENS, B., LEVICK, S. R. & SCHMULLIUS, C. 2014. Carbon stock and density of northern boreal and temperate forests. *Global Ecology and Biogeography,* 23**,** 297-310.

TIAN, H., LU, C., CIAIS, P., MICHALAK, A. M., CANADELL, J. G., SAIKAWA, E., HUNTZINGER, D. N., GURNEY, K. R., SITCH, S. & ZHANG, B. 2016. The terrestrial biosphere as a net source of greenhouse gases to the atmosphere. *Nature,* 531**,** 225-228.

TIESSEN, H. & MOIR, J. O. 1993. Characterization of available P by sequential extraction. *In:* CARTER, M. R. & GREGORICH, E. G. (eds.) *Soil sampling and methods of analysis.* Taylor & Francis Group.

TOKY, O. P. & RAMAKRISHNAN, P. S. 1983. Secondary succession following slash and burn agriculture in northeastern India 1. Biomass, litterfall and productivity. *Journal of Ecology,* 71**,** 735-745.

TOLEDO, M., POORTER, L., PEÑA‐CLAROS, M., ALARCÓN, A., BALCÁZAR, J., LEAÑO, C., LICONA, J. C., LLANQUE, O., VROOMANS, V. & ZUIDEMA, P. 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. *Journal of Ecology,* 99**,** 254-264.

TOLEDO, M. & SALICK, J. 2006. Secondary Succession and Indigenous Management in Semideciduous Forest Fallows of the Amazon Basin1. *Biotropica,* 38**,** 161-170.

TORELLO-RAVENTOS, M., FELDPAUSCH, T. R., VEENENDAAL, E., SCHRODT, F., SAIZ, G., DOMINGUES, T. F., DJAGBLETEY, G., FORD, A., KEMP, J. & MARIMON, B. S. 2013. On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions. *Plant Ecology & Diversity,* 6**,** 101-137.

TSCHAKERT, P., COOMES, O. T. & POTVIN, C. 2007. Indigenous livelihoods, slash-and-burn agriculture, and carbon stocks in Eastern Panama. *Ecological Economics,* 60**,** 807-820.
TUMMERS, B. 2006. Data Thief III. http://datathief.org/.
UHL, C. 1987. Factors Controlling Succession Following Slash-and-Burn Agriculture in Amazonia *Journal of Ecology,* 75**,** 377-407.
UHL, C., BUSCHBACHER, R. & SERRAO, E. A. S. 1988. Abandoned Pastures in Eastern Amazonia. I. Patterns of Plant Succession *Journal of Ecology,* 76**,** 663-681.
UHL, C., JORDAN, C., CLARK, K., CLARK, H. & HERRERA, R. 1982. Ecosystem Recovery in Amazon Caatinga Forest after Cutting, Cutting and Burning, and Bulldozer Clearing Treatments. *Oikos,* 38**,** 313-320.
UHL, C. & JORDAN, C. F. 1984. Succession and Nutrient Dynamics Following Forest Cutting and Burning in Amazonia. *Ecology,* 65**,** 1476-1490.
UHL, C. & KAUFFMAN, J. B. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern amazon. *Ecology,* 71**,** 437-449.
UNEP 2015. The Emissions Gap Report 2015. Nairobi: United Nations Environmental Program (UNEP).
UNFCCC 2010. Cancun agreements. *Report of the Conference of the Parties on its sixteenth session.* United Nations Framework Convention on Climate Change.
UNFCCC 2014. New York Declaration on Forest. New York: United Nations.
UNFCCC. The Paris Agreement. Conference of the Parties 21, 2015 Paris. United Nations Framework Convention on Climate Change.
URIARTE, M., YACKULIC, C. B., LIM, Y. & ARCE-NAZARIO, J. A. 2011. Influence of land use on water quality in a tropical landscape: a multi-scale analysis. *Landscape ecology,* 26**,** 1151-1164.
URQUIZA-HAAS, T., DOLMAN, P. M. & PERES, C. A. 2007. Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: Effects of forest disturbance. *Forest Ecology and Management,* 247**,** 80-90.
UWA-FACE 2007. Natural High Forest Rehabilitation Project on degraded land of Kibale National Park. *Verified Carbon Standard Project Description Template.*
UWA-FACE 2011. UWA-FACE the Future Annual Plan of Opperation. Fort Portal, Uganda: Uganda Wildlife Authority.
VALENCIA, R., BALSLEV, H. & MIÑO, G. P. Y. 1994. High tree alpha-diversity in Amazonian Ecuador. *Biodiversity & Conservation,* 3**,** 21-28.
VAN BREUGEL, M., HALL, J. S., CRAVEN, D., BAILON, M., HERNANDEZ, A., ABBENE, M. & VAN BREUGEL, P. 2013. Succession of ephemeral secondary forests and their limited role for the conservation of floristic diversity in a human-modified tropical landscape. *PloS one,* 8**,** e82433.
VAN BREUGEL, M., RANSIJN, J., CRAVEN, D., BONGERS, F. & HALL, J. S. 2011. Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. *Forest Ecology and Management,* 262**,** 1648-1657.
VAN DO, T., OSAWA, A. & THANG, N. T. 2010. Recovery process of a mountain forest after shifting cultivation in Northwestern Vietnam. *Forest ecology and management,* 259**,** 1650-1659.
VAN KLEUNEN, M., WEBER, E. & FISCHER, M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters,* 13**,** 235-245.
VAN NOORDWIJK, M., DEWI, S., KHASANAH, N., EKADINATA, A., RAHAYU, S., CALIMAN, J., SHARMA, M. & SUHARTO, R. 2010. Estimating carbon footprint from biofuel production from oil palm: methodology and results from 2 pilot areas in Indonesia. *International Conference of Oil Palm and Environment.* Bali, Indonesia.
VAN NOORDWIJK, M., RAHAYU, S., HAIRIAH, K., WULAN, Y. C., FARIDA, A. & VERBIST, B. 2002. Carbon stock assessment for a forest-to-coffee conversion landscape in

Sumber-Jaya (Lampung, Indonesia): from allometric equations to land use change analysis. *Science in China Series C-Life Sciences,* 45**,** 75-86.
VAN ORSDOL, K. G. 1986. Agricultural encroachment in Uganda's Kibale Forest. *Oryx,* 20**,** 115-117.
VAN REEUWIJK, L. P. 2002. Procedures for soil analysis. 6th Edition ed. The Netherlands: International Soil Reference and Information Centre.
VENTER, M., VENTER, O., LAURANCE, S. & BIRD, M. 2012. Recarbonization of the Humid Tropics. *In:* LAL, R., LORENZ, K., HÜTTL, R. F., SCHNEIDER, B. U. & VON BRAUN, J. (eds.) *Recarbonization of the Biosphere.* Springer Netherlands.
VISSEREN-HAMAKERS, I. J., MCDERMOTT, C., VIJGE, M. J. & CASHORE, B. 2012. Trade-offs, co-benefits and safeguards: current debates on the breadth of REDD+. *Current Opinion in Environmental Sustainability,* 4**,** 646-653.
VITOUSEK, P. M. & SANFORD, R. 1986. Nutrient cycling in moist tropical forest. *Annual review of Ecology and Systematics***,** 137-167.
WERNER, P. A. & MURPHY, P. G. 2001. Size-specific biomass allocation and water content of above-and below-ground components of three Eucalyptus species in a northern Australian savanna. *Australian Journal of Botany,* 49**,** 155-167.
WEST, T. A. P., VIDAL, E. & PUTZ, F. E. 2014. Forest biomass recovery after conventional and reduced-impact logging in Amazonian Brazil. *Forest Ecology and Management,* 314**,** 59-63.
WHEELER, C. E., OMEJA, P. A., CHAPMAN, C. A., GLIPIN, M., TUMWESIGYE, C. & LEWIS, S. L. 2016. Carbon sequestration and biodiversity following 18years of active tropical forest restoration. *Forest Ecology and Management,* 373**,** 44-55.
WHITMORE, T. C. 1984. *Tropical rain forests of the Far East* Oxford, Clarendon Press.
WHITMORE, T. C. 1998. *An introduction to tropical rain forests,* Oxford, Oxford University Press.
WILLIAMS-LINERA, G. 1983. Biomass and Nutrient Content in Two Successional Stages of Tropical Wet Forest in Uxpanapa, Mexico. *Biotropica,* 15**,** 275-284.
WILSON, E. O. 1987. The Little Things That Run the World (The Importance and Conservation of Invertebrates). *Conservation Biology,* 1**,** 344-346.
WINJUM, J. K., BROWN, S. & SCHLAMADINGER, B. 1998. Forest harvests and wood products: sources and sinks of atmospheric carbon dioxide. *Forest Science,* 44**,** 272-284.
WOLOSIN, M. 2014. Quantifying Benefits of the New York Declaration on Forests. Available at [http://www.climateadvisers.com/nydf/%5D.
WOODROFFE, R. & GINSBERG, J. R. 1998. Edge effects and the extinction of populations inside protected areas. *Science,* 280**,** 2126-2128.
WRI. 2015a. *African Forest Landscape Restoration Initiative (AFR100)* http://www.wri.org/our-work/project/AFR100/about-afr100 [Online]. [accessed July 2015].
WRI. 2015b. *Initiative 20X20* http://www.wri.org/our-work/project/initiative-20x20 [Online]. [accessed July 2015].
WRIGHT, S. J. 2013. The carbon sink in intact tropical forests. *Global change biology,* 19**,** 337-339.
YANG, X., BLAGODATSKY, S., LIPPE, M., LIU, F., HAMMOND, J., XU, J. & CADISCH, G. 2016. Land-use change impact on time-averaged carbon balances: Rubber expansion and reforestation in a biosphere reserve, South-West China. *Forest Ecology and Management,* 372**,** 149-163.
YUEN, J. Q., ZIEGLER, A. D., WEBB, E. L. & RYAN, C. M. 2013. Uncertainty in below-ground carbon biomass for major land covers in Southeast Asia. *Forest Ecology and Management,* 310**,** 915-926.

ZAHAWI, R. A. & HOLL, K. D. 2009. Comparing the performance of tree stakes and seedlings to restore abandoned tropical pastures. *Restoration Ecology,* 17**,** 854-864.

ZAHAWI, R. A., HOLL, K. D., COLE, R. J. & REID, J. L. 2013. Testing applied nucleation as a strategy to facilitate tropical forest recovery. *Journal of Applied Ecology,* 50**,** 88-96.

ZALUCKI, M., DAY, M. & PLAYFORD, J. 2007. Will biological control of *Lantana camara* ever succeed? Patterns, processes & prospects. *Biological Control,* 42**,** 251-261.

ZANNE, A. E., LOPEZ-GONZALEZ, G., COOMES, D.A., ILIC, J., JANSEN, S., LEWIS, S.L., MILLER, R.B., SWENSON, N.G., WIEMANN, M.C., AND CHAVE, J 2009. Global wood density database. http://hdl.handle.net/10255/dryad.235. : Dryad.

ZIEGLER, A. D., PHELPS, J., YUEN, J. Q., WEBB, E. L., LAWRENCE, D., FOX, J. M., BRUUN, T. B., LEISZ, S. J., RYAN, C. M., DRESSLER, W., MERTZ, O., PASCUAL, U., PADOCH, C. & KOH, L. P. 2012. Carbon outcomes of major land-cover transitions in SE Asia: great uncertainties and REDD plus policy implications. *Global Change Biology,* 18**,** 3087-3099.

Appendix 1 Metadata for each site used in systematic review. MAT = mean annual temperature (˚C), MAP = mean annual precipitation (mm), Dry ¼ = precipitation in driest quarter (mm), Age range = minimum and maximum plot age (years), Duration = duration of land use prior to abandonment (years), Method = study type, either chronosequence (C) or repeat measure (R), for repeat measure studies mean census interval in years is shown in parentheses. Soil group is from FAO-UNESCO soil classification system (IUSS working group WRB, 2014), Min DBH = minimum DBH cut-off used in study.

Site	Country	Lat/Long	MAT (˚C)	MAP (mm)	Dry ¼ (mm)	Original forest type	Land use type	Age range (yrs)	Duration (yrs)	Method	Soil group	Min DBH	Source
AID2	Puerto Rico	18.1, -66.1	222	1835	240	Tropical moist forest	Pasture	4-77		C	Cambisols	1	1
AID1	Puerto Rico	18.3, -65.8	241	2515	340	Tropical moist forest	Pasture	0-35	12.5-50	C	Cambisols	1	2
ALV	Brazil	-10.3, -62.8	249	2087	64	Tropical moist forest	Agriculture	2-18	1-6	C	Ferralsols	5	3
BRO	Bolivia	-11.4, -69.2	248	1778	115	Tropical moist forest	SC	4-47		C	Acrisols	2	4
CHA2	Uganda	0.4, 30.3	204	1304	196	Tropical moist forest	Agriculture	1-4		R (1)	Andosols	1	5
KNP	Uganda	0.3, 30.3	216	1124	163	Tropical moist forest	SC	10-18		R (8)	Nitosols	10	6
INF	Malaysia	5.0, 117.8	257	2341	520	Tropical moist forest	Logged	18-26		R (4)	Acrisols	10	7
CHA	Costa Rica	10.4, -84.0	261	3949	579	Tropical moist forest	Pasture	10-41		C	Acrisols	5	8
CIF	Costa Rica	10.3, -84.5	230	4123	331	Montane forest	Pasture	0.5-50		C	Andosols	10	9
COS	Brazil	-6.1, -49.9	262	1834	84	Tropical moist forest	Pasture	0-15		C	Ferralsols	10	10
DOL	Brazil	-9.9, -56.3	254	2252	44	Tropical moist forest	SC	7-8	0-1	C	Ferralsols	5	11
DAV	Brazil	-3, -47.5	263	1854	99	Tropical moist forest	Pasture	15-17		R (1)	Ferralsols	2	12
DEN	Panama	9.2, -79.9	262	2593	129	Tropical moist forest	Pasture	20-100		C	Planosols	5	13
DUP	Mexico	20.1, -89.5	257	1032	84	Tropical Dry Forest	SC	3-70		C	Luvisols	5	14
EAT	Mexico	18.9, -89.4	249	1096	96	Tropical Dry Forest	SC	2-25	1-7	C	Rendzinas	1	15
EWE	Malaysia	1.1, 110.8	270	3426	599	Tropical moist forest	SC	4.5-9.5		C	Acrisols	2	16
FEL	Brazil	-2.4, -60	270	2393	361	Tropical moist forest	Pasture	1-17	3-15	R (1)	Ferralsols	1	17
FON	Costa Rica	10.0, -83.2	263	3175	605	Tropical moist forest	Pasture	0-20		C	Regosols	2.5	18
FUK1	Myanmar	18.8, 95.9	254	1326	11	Tropical moist forest	SC	1-40		C	Nitosols	1	19
FUK2	Thailand	18.5, 98.5	224	947	32	Montane forest	SC	24.5-44.5		C	Acrisols	1	20
GEH	Brazil	-1.7, -60.3	267	2764	397	Tropical moist forest	SC	2-25		C	Ferralsols	0.2	21

Site	Country	Lat/Long	MAT (˚C)	MAP (mm)	Dry ¼ (mm)	Original forest type	Land use type	Age range (yrs)	Duration (yrs)	Method	Soil group	Min DBH	Source
HAR	Papua New Guinea	-6.6, 147	215	2330	484	Tropical moist forest	SC	0.4-1.9		R (0.3)	Cambisols	1	22
HAS	Indonesia	-0.3, 117	267	1978	337	Tropical moist forest	SC	1-11	1-9	C	Fluvisols	10	23
HUG	Mexico	18.6, -95.1	244	3404	221	Tropical moist forest	Agriculture	0.5-50	1-30	C	Andosols	10	24
JEP	Malaysia	3.6, 113.6	268	3577	735	Tropical moist forest	SC	1-15		C	Acrisols	3	25
JOH	Brazil	-1.2, -47.4	261	2469	106	Tropical moist forest	SC	10-40		C	Ferralsols	5/10	26
JUN	Brazil	-5.8, -61.6	266	2646	243	Tropical moist forest	SC	5-30		C	Gleysols	5	27
KEN	Bolivia	-16.8, -61.8	237	1047	93	Tropical Dry Forest	SC	1-50		C	Luvisols	5	28
KEN2	Malaysia	3.7, 113.7	267	3522	721	Tropical moist forest	SC	4-17		R (2)	Acrisols	3	29
KIY	Indonesia	0.3, 115.7	262	3253	573	Tropical moist forest	SC	33-34		R (1)	Acrisols	5	30
KOH	Indonesia	-0.9, 100.5	175	2139	293	Tropical moist forest	Logged	14.5-17.5		R (3)	Cambisols	5	31
KOH2	Indonesia	-0.9, 100.5	175	2139	293	Tropical moist forest	Agriculture	4-17.5		R (3)	Cambisols	5	31
LAS	Philippines	9.1, 126	239	4151	563	Tropical moist forest	Logged	3-63		C	Nitosols	19.5	32
LAW	Indonesia	0.1, 110	271	3038	536	Tropical moist forest	SC	9-12		C	Ferralsols	10	33
LEB	Mexico	16.7, -95	262	1001	24	Tropical Dry Forest	Agriculture	2-60		C	Phaeozems	5	34
LET	Costa Rica	10.4, -84	261	3981	573	Tropical moist forest	Pasture	10-44	0-20	C	Acrisols	2.5	35
LUSA	Indonesia	4, 117.1	270	2967	563	Tropical moist forest	Agriculture	1-15		C	Acrisols	1	36
LUSL	Indonesia	4, 117.1	270	2967	563	Tropical moist forest	Logged	1.5-40.5		C	Acrisols	1	36
MAD	Brazil	-14.9, -44	242	835	4	Tropical Dry Forest	Pasture	14-58		C	Luvisols	5	37
MAR	Puerto Rico	18, -66.1	235	1715	193	Montane forest	Pasture	10-60		C	Cambisols	10	38
MAZ	Brazil	-2.9, -47.8	270	2042	115	Tropical moist forest	Logged	1-4		R (2)	Ferralsols	10	39
MOR	Mexico	19.4, -104.9	259	852	13	Tropical Dry Forest	Pasture	3-15		C	Vertisols	1	40
NIN	Jamaica	17.9, -77.7	245	1685	160	Tropical dry forest	Logged	0-10		R (10)	Fluvisols	2	41
NOG	Brazil	-2.6, -60	271	2206	330	Tropical moist forest	Logged	7-10		R (4)	Ferralsols	5	42
OHT	Malaysia	6, 116.6	207	2198	372	Montane forest	SC	0.3-3		C	Acrisols	0.1	43
ORI	Mexico	17, -93.6	218	1123	74	Tropical moist forest	SC	2.5-35.5		C	Cambisols	2.5	44

Site	Country	Lat/Long	MAT (˚C)	MAP (mm)	Dry ¼ (mm)	Original forest type	Land use type	Age range (yrs)	Duration (yrs)	Method	Soil group	Min DBH	Source
PEN	Bolivia	-11.8, -67.3	261	1659	119	Tropical moist forest	SC	2-40		C	Acrisols	5	45
PIO	Brazil	-14.4, -39.1	240	1971	381	Atlantic forest	SC	10-40		C	Ferralsols	5	46
POW	Costa Rica	10.4, -85.4	266	1828	12	Tropical Dry Forest	Pasture	5-70		C	Gleysols	10	47
RAH	Madagascar	-20, 44.6	260	921	3	Tropical Dry Forest	SC	3-40		C	Arenosols	5	48
RIS	Indonesia	-0.4, 117.2	267	2070	405	Tropical moist forest	Agriculture	1.5-35		C	Regosols	10	49
RUI	Colombia	13.4, -81.4				Tropical Dry Forest	Agriculture	6-56		C		2.5	50
SAL	Venezuela	1.9, -67.1	262	3430	638	Tropical moist forest	SC	9-80		C	Gleysols	1	51
SAL2	Brazil	-10, -67.9	260	1942	126	Tropical moist forest	Pasture	6-35		C	Acrisols	1	52
SIE	Columbia	6.8, -75.1	231	2923	262	Tropical moist forest	Pasture	3-36		C	Fluvisols	10	53
SNE	Guatemala	15.6, -89.2	265	3054	259	Tropical moist forest	Pasture	1-10		C	Cambisols	1	54
STE1	Brazil	-3.4, -60.3	275	2197	230	Tropical moist forest	SC	5-30	1-14	C	Gleysols	5	55
STE2	Bolivia	-17.5, -63.5	243	1411	158	Tropical moist forest	SC	4-25	1-39	C	Lithosols	5	55
SZO	Peru	-5.8, -75.8	266	2093	333	Tropical moist forest	SC	0.3-4.4		R (1)	Ferralsols	2.5	56
TOL	Bolivia	-15.5, -63	254	1140	101	Tropical moist forest	SC	1-36		C	Luvisols	5	57
TOY	India	26, 91.1	246	1869	34	Montane forest	SC	1-20		C	Acrisols	7	58
TSC	Panama	9, -78.5	262	2031	48	Tropical moist forest	SC	1-12.5		C	Nitosols	5	59
UHL3	Venezuela	1.9, -67.1	262	3430	638	Tropical moist forest	SC	1-5		R (1)	Gleysols	2	60
UHL2	Venezuela	1.9, -67.1	262	3430	638	Tropical moist forest	SC	1-5		R (1)	Gleysols	2	61
UHL1	Brazil	-3, -47.4	264	1809	98	Tropical moist forest	Pasture	1-8	0-12	C	Ferralsols	2	62
URQ	Mexico	19.8, -88	259	1258	133	Tropical Dry Forest	SC	12.5-50		C	Cambisols	10	63
VAB1	Panama	9.2, -79.8	259	2757	130	Tropical moist forest	Pasture	2-31		C	Histosols	5	64
VAB2	Mexico	16.1, -90.8	255	2959	217	Tropical moist forest	SC	0-27		C	Acrisols	1	65
VAN	Vietnam	21.4, 103.6	169	1809	37	Tropical moist forest	SC	5-26		C	Acrisols	1	66
VAN2	Indonesia	-5, 104.3	210	2853	385	Tropical moist forest	SC	1-20		C	Andosols	5	67
WIL	Mexico	17.1, -94.4	229	2342	229	Tropical moist forest	Agriculture	0.8-7		C	Lithosols	1	68

1 = Aide et al. (2000), 2 = Aide et al. (1995), 3 = Alves et al. (1997), 4 = Broadbent et al. (2014), 5 = Chapman and Chapman (1999), 6 = Chapter 3 data, 7 = Chapter 4 data, 8 = Chazdon et al. (2005), 9 = Cifuentes-Jara (2008), 10 = Costa et al. (2012), 11 = d'Oliveira et al. (2011), 12 = Davidson et al. (2004), 13 = Denslow and Guzman (2000), 14 = Dupuy et al. (2012), 15 = Eaton and Lawrence (2009), 16 = Ewel et al. (1983), 17 = Feldpausch et al. (2007), 18 = Fonseca et al. (2011), 19 = Fukushima et al. (2007), 20 = Fukushima et al. (2008), 21 = Gehring et al. (2005), 22 = Hartemink (2001), 23 = Hashimotio et al. (2000), 24 = Hughes et al. (1999), 25 = Jepsen (2006), 26 = Johnson et al. (2001), 27 = Junqueira et al. (2010), 28 = Kennard (2002), 29 = Kenzo et al. (2010), 30 = Kiyono (2005), 31 = Kohyama et al. (1989), 32 = Lasco et al. (2006), 33 = Lawrence (2005), 34 = Lebrija‐Trejos et al. (2008), 35 = Letcher and Chazdon (2009), 36 = Lusiana and van Noordwijk (2005), 37 = Madeira et al. (2009), 38 = Marin-Spiotta et al. (2007), 39 = Mazzei et al. (2010), 40 = Mora et al. (2015), 41 = Niño et al. (2014), 42 = Nogueira Lima et al. (2007), 43 = Ohtsuka (2001), 44 = Orihuela-Belmonte et al. (2013), 45 = Peña‐Claros (2003), 46 = Piotto (2011), 47 = Powers et al. (2009), 48 = Raharimalala et al. (2012), 49 = Riswan (1985), 50 = Ruiz et al. (2005), 51 = Saldarriaga et al. (1988), 52 = Salimon and Brown (2000), 53 = Sierra et al. (2012), 54 = Snedaker (1970), 55 = Steininger (2000), 56 = Szott et al. (1994), 57 = Toledo and Salick (2006), 58 = Toky and Ramakrishnan (1983), 59 = Tschakert et al. (2007), 60 = Uhl (1987), 61 = Uhl and Jordan (1984), 62 = Uhl et al. (1988), 63 = Urquiza-Haas et al. (2007), 64 = van Breugel et al. (2013), 65 = van Breugel et al. (2011), 66 = Van Do et al. (2010), 67 = van Noordwijk et al. (2002), 68 = Williams-Linera (1983).

Appendix 2. Number of individuals of each species originally planted per ha in each compartment, compartment size (ha) and median planting month. Asterisks indicate the planted species (≥1 cm DBH) that were seen in 2013. Species in bold are the two most commonly planted species found in 2013.

Compartment	101	102	103	107	108	109	113	114	Mean stems planted (per ha)
Compartment area (ha)	62.5	225	65	75	84	56.5	75	86	
Median Planting month	03/95	03/95	03/95	09/95	09/95	03/06	03/06	09/96	
Species									
Markhamia platycalyx	76.7	76.8	74.9	82.2	32.9	47.4	48.5	39.7	59.9
Uvariopsis congensis	38.6	38.4	37.1	44.2	58.9	95.6	98.5	18.8	53.8
Prunus africana	59.2	59.4	59.0	57.6	10.1	16.3	7.8	99.2	46.1
Mimusops bagshawei	65.3	65.8	62.8	63.5	69.0	-	1.5	3.9	47.4
Lavoa brownii	23.6	23.5	16.5	22.9	93.8	42.5	43.3	11.9	34.8
Chrysophyllum albidum	10.4	10.4	8.1	10.1	45.3	25.4	26.5	2.3	17.3
Blaghia wildmaniana	13.0	13.0	12.5	18.6	18.4	30.5	27.8	3.9	17.2
Warburgia ugandensis	**0.9**	**0.9**	**2.4**	**0.9**	**19.2**	**21.4**	**41.5**	**58.5**	**18.2**
Strombosia scheffleri	18.6	18.9	17.4	18.1	1.4	10.1	9.4	-	13.4
Albizia gummifera	19.4	19.3	24.8	18.9	-	-	0.2	-	16.5
Bridelia micrantha	**13.0**	**0.0**	**-**	**-**	**4.3**	**0.4**	**0.4**	**73.9**	**15.3**
Diospyros mespiliformis	-	0.2	0.2	0.2	7.6	35.4	32.9	24.2	14.4
Antiaris toxicaria	1.6	14.4	14.0	14.1	9.3	-	-	-	10.7
Spathodea campanulata	13.4	13.4	12.9	17.1	-	1.6	1.7	-	10.0
Pancovia turbinata	9.3	9.2	8.6	9.0	-	-	12.5	3.9	8.8
Dasylepsis egglingii	-	-	-	-	-	11.6	12.1	38.4	20.7
Funtumia elastica	0.4	0.4	0.4	0.4	0.6	15.9	16.8	15.5	6.3
Celtis durandii	9.5	9.5	9.5	2.7	-	-	-	-	7.8
Aphania senegalensis	5.2	5.2	5.0	5.1	-	1.7	1.3	-	3.9
Blaghia unijugata	6.1	6.1	5.7	-	-	-	-	-	6.0
Trichilia dregeana	4.7	4.7	3.0	4.6	-	-	0.5	-	3.5
Monodora myristica	2.3	2.3	1.8	2.2	7.2	-	-	-	3.2
Tabernaemontana holstii	**-**	-	-	-	17.5	-	-	-	17.5
Balanites wilsoniana	3.6	3.3	2.3	3.5	-	-	0.4	-	2.6
Albizia cerria	-	0.0	-	-	10.3	0.2	0.2	-	2.7
Cordia mellenii	0.1	0.1	0.2	0.1	1.3	1.1	1.1	6.0	1.3
Trichilia africana	0.7	0.7	0.7	0.7	-	5.5	5.7	-	2.3
Fagaropsis angolensis	1.0	1.0	1.3	0.9	-	-	1.4	-	1.1
Phonix	0.8	0.8	1.0	0.8	-	-	-	-	0.8
Dictyandra arborescens	0.8	0.8	0.8	0.2	-	-	-	-	0.6
Pariniri excelsa	0.4	0.4	0.3	0.4	-	1.2	4.0	-	1.1
Aningeria altissma	0.3	0.3	0.3	0.3	-	?	1.2	-	0.5

Zanha golungensis	-	-	-	-	-	-	2.8	-	2.8
Newtonia buchannii	0.3	0.3	0.8	0.3	-	-	-	-	0.4
? Unknown Sp1	-	-	-	-	-	2.7	-	-	2.7
Cola gigantai	-	-	-	-	-	2.6	-	-	2.6
? Unknown Sp2	-	-	-	-	-	1.7	-	-	1.7
? Unknown Sp3	-	-	-	-	-	1.5	-	-	1.5
Teclea nobilis	0.2	0.2	0.2	0.2	-	-	-	-	0.2
? Unknown Sp4	-	-	-	-	-	1.3	-	-	1.3
Olea hostii	0.2	0.2	0.2	0.2	-	-	-	-	0.2
? Unknown Sp5	-	-	-	-	-	1.2	-	-	1.2
Moros leaves	0.1	0.1	0.1	0.1	-	-	-	-	0.1
Diospyros abyssinica	0.2	-	-	-	-	-	-	-	0.2
? Unknown Sp6	-	-	-	-	-	0.2	-	-	0.2
? Unknown Sp7	-	-	-	-	-	?	-	-	0.0
? Unknown Sp8	-	-	-	-	-	?	-	-	0.0
Trees planted (per ha)	400	400	385	400	407	375	400	400	480.7

Appendix 3: Number of planted individuals (per ha) encountered in 2013 per compartment.

Compartment	101	102	103	107	108	109	113	114	Total
Area sampled (ha)	0.25	0.25	0.35	0.25	0.35	0.35	0.35	0.35	2.5
Species									
Bridelia micrantha	68	80	103	144	146	29	66	77	89
Warburgia ugandensis	36	24	37	20	37	57	51	54	40
Sapium ellipticum	8	12	0	0	3	20	14	23	10
Mimusops bagshawei	4	-	37	-	6	-	-	-	16
Prunus africana	8	8	-	-	3	20	-	-	10
Tabernaemontana holstii	-	-	-	-	-	14	-	11	13
Croton macrostachyus	-	4	-	-	17	-	3	-	8
Markhamia lutea	-	-	-	-	-	17	-	3	10
Diospyros abyssinica	-	-	-	-	-	-	-	9	9
Uvariopsis congensis	-	-	-	-	-	3	-	3	3
Albizia grandibracteata	-	-	-	-	-	-	3	-	3
Allophyllus rubifolius	-	4	-	-	-	-	-	-	4
Blighia unijugata	-	-	3	-	-	-	-	-	3
Celtis durandii	-	-	-	-	3	-	-	-	3
Spathodea campanulata	4	-	-	-	-	-	-	-	4
Total individuals in sampled area	128	132	180	164	214	160	137	180	162

Appendix 4. Full species list of trees and seedlings in Kibale National Park showing; wood density and taxonomic level of wood density (S=species, G=genus, F=family, P=plot averaged wood density). Species code used for NMDS is also show, species with no code were only measured as seedlings and therefore were not included in NMDS analysis. Planted species are shown in bold, *= Only local name known, no scientific name.

Family	Species	Species code (NMDS)	Wood density (g cm^3)	Wood density level
Fabaceae	*Acacia hokkii*	Ac Spp	0.773	G
Fabaceae	*Acacia spp.*	Ac Spp	0.773	G
Fabaceae	*Albizia grandibracteata*	A.gra	0.570	S
Fabaceae	***Albizia gummifera***	**A.gum**	**0.500**	**S**
Sapindaceae	*Allophyllus rubifolius*	A.rub	0.482	G
Sapotaceae	*Aningeria altissma*	A.alt	0.533	S
Moraceae	***Antiaris toxicaria***		**0.390**	**S**
Euphorbiaceae	*Antidesma membranaceum*	A.mem	0.663	G
Sapindaceae	*Aphania senegalensis*	A.sen	0.752	S
Icacinaceae	*Apodytes dimidiata*		0.600	S
Balanitaceae	*Balanites wilsoniana*		0.580	G
Fabaceae	*Baphiopsis parviflora*	B.par	0.678	F
Fabaceae	*Bequaertiodendron natalense*	B.nat	0.702	F
Milianthaceae	*Bersama abyssinica*		0.617	S
Sapindaceae	*Blighia unijugata*	B.uni	0.573	S
Moraceae	*Bosqueia phoberos*	B.pho	0.640	S
Phyllanthaceae	***Bridelia micrantha***	**B.mic**	**0.510**	**S**
Phyllanthaceae	*Bridelia mildbraedii*	B.mil	0.521	G
Meliaceae	*Carapa grandiflora*		0.550	S
Apocynaceae	*Carissa edulis*		0.834	S
Leguminosae	*Cassia spectabilis*	C.spe	0.480	S
Rhizophoraceae	*Cassipourea ruwensorens*	C.ruw	0.649	G
Cannabaceae	*Celtis africana*	C.afr	0.652	S
Cannabaceae	*Celtis durandii*	C.dur	0.559	G
Cannabaceae	*Celtis mildbraedii*	C.mil	0.391	S
Cannabaceae	*Celtis zenkeri*	C.zen	0.609	S
Unknown	*Cena **	Cena	0.545-0.64	P
Ulmaceae	*Chaetacme aristata*	C.ari	0.559	S
Sapotaceae	*Chrysophyllum albidum*	C.alb	0.533	S
Rutaceae	*Citrus x lemon*		0.740	S
Rutaceae	*Clausena* Spp		0.573	S
Rubiaceae	*Coffea eugenioides*		0.633	S
Malvaceae	*Cola gigantea*		0.480	S

Family	*Species*	Species code (NMDS)	Wood density (g cm^3)	Wood density level
Combretaceae	*Combretum molle*	C.mol	0.758	S
Boraginaceae	*Cordia africana*		0.450	S
Leguminosae	*Craibia* Spp	Crab	0.619	G
Rubiaceae	*Craterisperum laurinum*		0.663	G
Euphorbiaceae	*Croton macrostachyus*	C.mac	0.633	S
Euphorbiaceae	*Croton megalocarpus*	C.meg	0.633	S
Fabaceae	*Cynometra alexandri*	C.ale	0.744	S
Unknown	*Cytropsis **		0.575-0.652	P
Flacourtiaceae	*Dasylepis eggelingii*	D.egg	0.679	S
Rubiaceae	*Dictyandra arborescens*	D.arb	0.619	S
Ebenaceae	***Diospyros abyssinica***	**D.aby**	**0.702**	**S**
Malvaceae	*Dombeya* Spp	D.mic	0.484	G
Flacourtiaceae	*Dovyalis microcarpa*	Dov.mic	0.579	G
Boraginaceae	*Ehretia cymosa*	E.cym	0.521	S
Fabaceae	*Erythrina abyssinica*	E.aby	0.426	S
Capparidaceae	*Euadenia eminens*	E.emi	0.419	S
Rutaceae	*Fagara angolensis*		0.592	S
Rutaceae	*Fagaropsis angolensis*		0.504	S
Moraceae	*Ficus capensis*	F.cap	0.288	S
Moraceae	*Ficus exasperata*	F.exa	0.344	S
Moraceae	*Ficus natalensis*	F.nat	0.442	G
Moraceae	*Ficus urceolaris*		0.442	G
Flacourtiaceae	*Flacourtia indica*		0.737	S
Apocynaceae	*Funtumia africana*	F.afr	0.500	S
Apocynaceae	*Funtumia latifolia*	F.lat	0.424	G
Rubiaceae	*Gardenia lanciloba*	G.lan	0.671	G
Tiliaceae	*Grewia occidentalis*	G.occ	0.426	G
Simaroubaceae	*Harrisonia abyssinica*	H.aby	0.785	G
Aquifoliaceae	*Ilex mitis*		0.468	S
Bignoniaceae	*Kigelia africana*	K.afr	0.464	S
Bignoniaceae	*Kigelia moosa*	k.moo	0.632	G
Olacaceae	*Lenosera* Spp		0.757	F
Sterculiaveae	*Leptonychia mildbreadii*	L.mil	0.598	S
Flacourtiaceae	*Lindackeria* Spp		0.669	S
Meliaceae	***Lovoa brownii***	**L.bro**	**0.623**	**G**
Myrsinaceae	*Maesa lanceolata*		0.676	S
Anacardiaceae	*Mangifera indica*	M.ind	0.536	S
Euphorbiaceae	*Margaritaria discoidea*	M.dis	0.618	S
Bignoniaceae	*Markhamia lutea*	M.lut	0.475	S
Bignoniaceae	***Markhamia platycalyx***	**M.pla**	**0.500**	**S**
Fabaceae	*Millettia dura*	M.dur	0.698	S

Family	*Species*	Species code (NMDS)	Wood density (g cm^3)	Wood density level
Sapotaceae	***Mimusops bagshawei***	**M.bag**	**0.768**	**S**
Unknown	*Mintnencea andata*	M.and	0.51-0.652	P
Rubiaceae	*Mitragyna rubrostipulata*	M.rub	0.537	S
Annonaceae	*Monodora myristica*	M.myr	0.490	G
Apocynaceae	*Motandra guineensis*	M.gui	0.567	F
Euphorbiaceae	*Neoboutonia melleri*		0.292	S
Fabaceae	*Newtonia buchananiI*	New	0.496	S
Ochnaceae	*Ochna holstii*	O.ton	0.745	S
Oleaceae	*Olea capensis*		0.774	S
Oleaceae	*Olea wilwichai*		0.718	S
Flacourtiaceae	*Oncoba spinosa*		0.580	S
Rubiaceae	*Oxyanthus* Spp		0.525	S
Sapindaceae	***Pancovia turbinata***		**0.783**	**S**
Chrysobalanaceae	*Pariniri excelsa*	P.exc	0.605	S
Lauraceae	*Persea americana*	P.ame	0.523	S
Palmae	*Phoenix reclinata*	Phon	0.685	F
Leguminosae	*Piptadeniastrum*	Pipt	0.605	S
Pittosporaceae	*Pittosporum*		0.621	G
Apocynaceae	*Pleiocarpa pycnantha*	P.pyc	0.683	S
Lamiaceae	*Premna angolensis*	P.ang	0.525	S
Rosaceae	***Prunus africana***	**P.afr**	**0.552**	**S**
Anacardiaceae	*Pseudospondias microcarpa*		0.623	S
Myrtaceae	*Psidium guajava*		0.625	S
Unknown	*pterygota **		0.550	G
Rubiaceae	*Randia* Spp		0.657	G
Apocynaceae	*Rauvolfia vomitoria*	R.vom	0.472	G
Rubiaceae	*Rothmannia* Spp		0.600	S
Euphorbiaceae	*Sapium ellipticum*	S.ell	0.551	S
Flacourtiaceae	*Scolopia rhamnophylla*		0.635	S
Bignoniaceae	***Spathodea campanulata***	**S.cam**	**0.234**	**S**
Unknown	*Spinosis **		0.510	P
Olacaceae	***Strombosia scheffleri***	**S.sch**	**0.699**	**S**
Loganiaceae	*Strychnos mitis*	S.mit	0.722	S
Clusiaceae	*Symphonia globulifera*		0.756	S
Apocynaceae	*Tabernaemontana holstii*	T.hol	0.539	G
Apocynaceae	*Tabernaemontana johnsonii*		0.539	G
Rutaceae	*Teclea nobilis*	T.nob	0.745	S
Moraceae	*Treculia africana*	Trec	0.541	F
Cannabaceae	*Trema guineensis*	T.gui	0.336	G
Meliaceae	*Trichilia africana*	T.afr	0.512	G
Meliaceae	*Trichilia dregeana*	T.pri	0.482	S

Family	*Species*	Species code (NMDS)	Wood density (g cm^3)	Wood density level
Meliaceae	*Trichilia prieuriana*		0.663	S
Annonaceae	***Uvariopsis congensis***	**U.con**	**0.661**	**S**
Rubiaceae	*Vanguaoria apiculata*	V.api	0.657	G
Aquifoliaceae	*Vernonia mangandelena*	V.man	0.330	G
Canellaceae	***Warburgia ugandensis***	**W.uga**	**0.689**	**G**
Sapindaceae	*Zanha golungensis*	Z.gol	0.732	S

Appendix 5. Number of non-planted individuals (per ha) encountered in 2005 and 2013 per compartment

	2005								2013							
Compartment	101	102	103	107	108	109	113	114	101	102	103	107	108	109	113	114
Species																
Acacia spp	4	-	11	16	-	-	-	6	-	-	-	4	-	-	-	-
Acanthus pubecens	-	-	-	-	-	-	-	-	-	4	3	-	31	-	-	-
Albizia grandibracteata	-	-	9	-	3	3	6	6	-	-	-	-	6	3	3	3
Albizia gummifera	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-
Allophyllus rubifolius	-	-	-	-	-	9	-	-	-	-	-	-	-	26	-	-
Antidesma membranaceum	-	-	-	-	-	6	3	-	-	-	-	-	-	9	-	3
Aphania senegalensis	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-
Bridelia micrantha	4	16	23	-	3	6	14	9	12	20	40	48	20	6	37	74
Bridelia mildbraedii	-	-	-	-	-	-	-	-	16	-	-	-	-	-	-	-
Cassia spectabilis	-	-	-	-	-	3	3	-	-	-	-	-	-	-	-	-
Celtis durandii	-	-	-	-	3	-	-	-	-	-	3	-	3	11	3	-
Cena	-	-	-	-	-	-	-	-	-	-	-	-	6	3	-	-
Chrysophyllum albidum	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-
Combretum molle	-	-	-	12	-	-	14	17	-	-	-	28	-	-	14	40
Diospyros abyssinica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	-
Dovyalis microcarpa	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Erythrina abyssinica	-	8	6	4	3	-	-	3	-	12	6	4	3	-	-	6
Ficus capensis	4	4	11	-	3	-	-	-	-	-	-	-	-	-	-	-
Ficus natalensis	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
Funtumia africana	-	-	-	-	-	3	-	-	8	-	-	-	-	11	3	-
Gardenia lanciloba	8	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-
Grewia occidentalis	4	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
Harrisonia abyssinica	-	-	-	-	-	-	9	3	-	-	-	-	-	6	14	14
Lavoa brownii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Mangifera indica	-	-	-	-	-	-	-	3	-	-	-	-	-	-	3	6

Mintnencea andata	-	-	-	-	-	-	-	-	-	-	-	-	-	3	6	-
Persea americana	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Premna angolensis	-	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-
Prunus africana	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-
Rauvolfia vomitoria	-	4	6	-	-	3	3	3	-	4	6	-	3	6	6	3
Sapium ellipticum	20	44	3	4	3	29	40	20	52	64	43	16	20	77	66	57
Securinega virosa	-	-	-	-	-	-	-	-	-	-	3	-	11	3	-	9
Spathodea campanulata	-	-	-	-	-	-	-	-	-	-	-	-	6	6	3	-
Vanguoria apiculata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	3
Vanonia Spp	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
Vernonia mangandelena	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Warburgia ugandensis	-	-	-	-	-	-	-	-	4	-	-	-	-	-	14	-
Total individuals (per ha)	44	76	74	40	17	60	91	71	96	108	106	100	126	171	186	220

Appendix 6. Details of compartment area (ha), area of compartment that received planting (ha), the total number of seedlings planted and species planted in restoration forest plots

	High				Mid				Low			
Compartment details	143	144	145	183	159	162	173	190	160	181	187	214
Compartment area (ha)	34	67	67	57	65	57	65	57	59	81	50	41
Area planted (ha)	14.9	1.7	1.7	2.4	7.1	8.9	7.1	8.9	2.9	5.7	2	2.9
Total seedlings planted	4948	565	565	802	2346	2951	2346	2951	961	1888	654	974
Seedling planted (per ha)	333	332	332	333	333	332	333	332	333	333	334	334
Species planted												
Dipterocarpus conformis												Y
Dryobalanops lanceolata	Y	Y	Y	Y	Y	Y	Y	Y	Y		Y	Y
Fruit spp.						Y		Y				
Hopea beccariana									Y			
Hopea nervosa	Y	Y	Y	Y		Y		Y		Y	Y	
Hopea sangal	Y	Y	Y	Y	Y	Y	Y	Y		Y	Y	Y
Parashorea malaanonan				Y		Y		Y	Y			Y
Parashorea tomentella	Y	Y	Y	Y		Y		Y	Y	Y	Y	
Shorea faguetiana	Y	Y	Y	Y		Y		Y	Y	Y	Y	
Shorea falceferoides					Y		Y					
Shorea fallax	Y	Y	Y	Y	Y		Y		Y	Y	Y	Y
Shorea gibbosa											Y	
Shorea johorensis	Y			Y	Y	Y	Y	Y	Y		Y	
Shorea leprosula	Y			Y		Y		Y	Y			
Shorea ovalis		Y	Y						Y	Y		Y
Shorea parvifolia		Y	Y	Y		Y		Y	Y		Y	
Shorea smithiana										Y		

Appendix 7. Estimates of total carbon storage per compartment. 2015 AGB calculated using AGB baseline of 200 Mg ha^{-1}, an AGB accumulation of 3.5 mg ha^{-1} yr^{-1} from year of logging - year of planting and an AGB accumulation of 7.8 Mg ha^{-1} yr^{-1} from year of planting to 2015.

Year Logged	Year planted	Compartment Area (ha)	2015 AGB (Mg ha^{-1})	Total AGB (per compartment)	Total C (per compartment)
1978	1993	109	424.1	46,227	21,773
1981	1993	56	415.5	38,226	18,004
1988	1993	108	413.6	23,162	10,909
1991	1993	57	409.3	88,818	41,833
1981	1994	217	392.1	152,919	72,025
1988	1994	482	366.3	157,875	74,359
1991	1994	27	397.2	222,829	104,953
1978	1995	92	392.9	587,778	276,844
1983	1995	409	398	162,782	76,670
1988	1995	866	393.7	214,960	101,246
1982	1996	561	371.1	252,719	119,031
1983	1996	546	366.8	15,039	7,083
1982	1997	1496	389.1	42,023	19,793
1981	1998	390	384.8	185,474	87,358
1987	1998	681	380.5	329,513	155,201
1988	1998	351	367.6	129,028	60,772
1987	1999	41	363.3	67,211	31,656
1988	1999	185	359.8	426,003	200,648
1989	1999	1184	355.5	211,523	99,627
1989	2000	595	352	402,336	189,500
1990	2000	1143	378.6	21,580	10,164
1991	2002	84	374.3	10,106	4,760
1991	2003	157	339.9	28,552	13,448
1981	2004	431	335.6	52,689	24,817
1991	2004	466	331.3	154,386	72,716
1987	2005	640	341	218,240	102,791
1987	2006	67	336.7	22,559	10,625
		11441.3		**4,264,556**	**2,008,606**
					2.01 Tg C

Appendix 8. Estimation of carbon additionality, calculated using the difference in AGB accumulation with and without restoration treatment. Shows total AGB accumulated per ha since restoration, total AGB and carbon accumulated since restoration across the entire compartment area and the difference between the with and without restoration scenarios. With restorations scenario used AGB accumulation rate of 7.8 Mg ha^{-1} yr^{-1}, whilst without restoration scenario used a rate of 3.5 Mg ha^{-1} yr^{-1}. * = Median AGB (Mg ha^{-1}) accumulated.

Compartment Details		AGB accumulation WITH RESTORATION			AGB accumulation WITHOUT RESTORATION			Difference	
Year planted	Area	AGB (Mg ha^{-1})	AGB (Mg - total area)	C (Mg - total area)	AGB (Mg ha^{-1})	AGB (Mg - total area)	C (Mg - total area)	AGB (Mg - total area)	C (Mg - total area)
1993	330	156	51,546	24,432	77	25,410	12,044	26,136	12,388
1994	726	149	108,247	51,309	74	53,362	25,293	54,885	26,016
1995	1367	142	194,114	92,010	70	95,690	45,358	98,424	46,653
1996	1107	135	149,334	70,785	67	73,616	34,893	75,718	35,891
1997	1496	128	191,189	90,623	63	94,248	44,674	96,941	45,950
1998	1422	121	171,636	81,355	60	84,610	40,104	87,026	41,250
1999	1410	114	160,176	75,924	56	78,960	37,427	81,216	38,496
2000	1738	107	185,098	87,736	53	91,246	43,251	93,852	44,486
2002	84	92	7,753	3,675	46	3,822	1,812	3,931	1,863
2003	157	85	13,376	6,340	42	6,594	3,126	6,782	3,215
2004	897	78	70,056	33,206	39	34,535	16,369	35,522	16,837
2005	640	71	45,440	21,539	35	22,400	10,618	23,040	10,921
2006	67	64	4,297	2,037	32	2,118	1,004	2,179	1,033
Total	**11441**	117*	**1,352,261**	**640,972**	58*	**666,607**	**315,972**	**685,653**	**324,999**
(95% CI)		(3.1)	(724)	(343)	(1.5)	(357)	(169)	(367)	(174)

Appendix 9. National restoration commitments in millions of ha (Mha). When stated, the area committed to each restoration method is given, plus percentage of total land area committed to each restoration method. 95% CI in parentheses. a = assisted natural regeneration involves management to enhance natural regeneration, including: fire control, enrichment planting and liberation thinning. b = abandoned agricultural fallows. c = protective lands including: erosion control and watershed protection. d = source of commitments either from BONN challenge website [http://www.bonnchallenge.org/], FLR desk, found on BONN challenge website [http://www.bonnchallenge.org/flr-desk], or from intended nationally determined contributions presented at COP21 in Paris 2015.

		Restoration method (Mha)							
Country	Commitment (Mha)	Plantation	Natural Regeneration	Assisted Natural Regeneration [a]	Agroforestry	Improved Fallow [b]	Mangrove	Protection [c]	Source [d]
Argentina	1.0								BONN
Bolivia	6.0								INDC
Brazil	23.1	19.0			4.1			0.0	FLR Desk
Burkina Faso	1.2	0.1		0.1	1.0			0.1	FLR Desk
Burundi	2.0								FLR Desk
Chile	0.6	0.1		0.4	0.1				FLR Desk
China	40.0	15.6	0.01	0.1	0.003			0.1	INDC
Columbia	2.0	1.0	1.0						FLR Desk
Costa Rica	1.2	0.1	0.2						BONN
Cote d'Ivoire	2.1	0.2	0.1	1.8					FLR Desk
DRC	16.8	13.0	0.1	1.3	2.4				FLR Desk
Ecuador	0.5								BONN
El Salvador	1.0				1.0				FLR Desk
Ethiopia	15.0	5.9	3.9	4.5					BONN
Ghana	1.7	1.1		0.5	0.03				FLR Desk
Guatemala	1.2	0.2	0.01	0.3	0.3		0.01	0.01	BONN
Honduras	1.0								BONN

India	13.0	0.3	0.8	5.5	3.0	0.6	0.1	0.1	BONN
Indonesia	28.9	16.6		6.2	0.0		0.0	6.0	FLR Desk
Kenya	5.1	4.1		0.0	0.1				BONN
Lao PDR	7.6	0.05	7.0	0.5					FLR Desk
Liberia	1.0								BONN
Madagascar	1.0								BONN
Mexico	10.5	3.6		6.8			0.01	0.04	FLR Desk
Mozambique	1.0								BONN
Nicaragua	2.8								BONN
Niger	3.2								BONN
Nigeria	30.0	13.8	0.4	0.1	15.7		0.1	0.01	BONN
Peru	3.2	1.2		0.0	0.6				BONN
Republic of Congo	2.0	1.0					0.0		BONN
Rwanda	2.0			0.003	1.6				BONN
Sri Lanka	0.2								INDC
Uganda	2.9	2.1		0.7	0.01			0.02	FLR Desk
Vietnam	17.3	2.7	0.8	13.8			0.1		FLR Desk
Zambia	0.1	0.1		0.02	0.02				FLR Desk
Total	248.1	101.9	14.2	42.5	29.9	0.6	0.4	6.4	
% Of Total area		44.8 (13.3)	10.7 (9.7)	22.1 (11)	20.7 (12.5)	0.2 (0.5)	0.1 (0.1)	1.3 (1.7)	

Appendix 10. Publication from Chapter 3: Wheeler CE, Omeja PA, Chapman CA, Glipin M, Tumwesigye C, & Lewis SL (2016) Carbon sequestration and biodiversity following 18years of active tropical forest restoration. *Forest Ecology and Management.* **373**: 44-55

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Carbon sequestration and biodiversity following 18 years of active tropical forest restoration

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ABSTRACT

Vast areas of degraded tropical forest, combined with increasing interest in mitigating climate change and conserving biodiversity, demonstrate the potential value of restoring tropical forest. However, there is a lack of long-term studies assessing active management for restoration. Here we investigate Above-Ground Biomass (AGB), forest structure, and biodiversity, before degradation (in old-growth forest), after degradation (in abandoned agricultural savanna grassland), and within a forest that is actively being restored in Kibale National Park, Uganda. In 1995 degraded land in Kibale was protected from fire and replanted with native seedlings (39 species) at a density of 400 seedlings ha^{-1}. Sixty-five plots (50 m × 10 m) were established in restoration areas in 2005 and 50 of these were re-measured in 2013, allowing changes to be assessed over 18 years. Degraded plots have an Above Ground Biomass (AGB) of 5.1 Mg dry mass ha^{-1}, of which 80% is grass. By 2005 AGB of trees ≥10 cm DBH was 9.5 Mg ha^{-1}, increasing to 40.6 Mg ha^{-1} by 2013, accumulating at a rate of 3.9 Mg ha^{-1} year^{-1}. A total of 153 planted individuals ha^{-1} (38%) remained by 2013, contributing 28.9 Mg ha^{-1} (70%) of total AGB. Eighteen years after restoration, AGB in the plots was 12% of old-growth (419 Mg ha^{-1}). If current accumulation rates continue restoration forest would reach old-growth AGB in a further 96 years. Biodiversity of degraded plots prior to restoration was low with no tree species and 2 seedling species per sample plot (0.05 ha). By 2005 restoration areas had an average of 3 tree and 3 seedling species per sample plot, increasing to 5 tree and 9 seedling species per plot in 2013. However, biodiversity was still significantly lower than old-growth forest, at 8 tree and 16 seedling species in an equivalent area. The results suggest that forest restoration is beneficial for AGB accumulation with planted stems storing the majority of AGB. Changes in biodiversity appear slower; possibly due to low stem turnover. Overall this restoration treatment is an effective means of restoring degraded land in the area, as can be seen from the lack of regeneration in degraded plots, which remain low AGB and diversity, largely due to the impacts of fire and competition with grasses.

1. Introduction

Large areas of forest lands have been converted to other land uses, and large areas of degraded tropical forest exists, covering some 550 million ha by some estimates (Pan et al., 2011). Degraded forests and abandoned agricultural lands have the potential to recover back to higher carbon and biodiversity value forest if left to regenerate naturally. However, natural regeneration is often arrested in very heavily degraded lands (Lowes and Chapman,

Abbreviations: UWA-FACE, Uganda Wildlife Authority and FACE (Forest absorbing carbon emissions) the forest foundation forest rehabilitation project; KNP, Kibale National Park; AGB, Above Ground Biomass; DBH, diameter at breast height; NMDS, non-metric multi-dimensional scaling; AGWP, above-ground wood production.

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2006; Paul et al., 2004). One of the major factors leading to arrested succession is the increased susceptibility of degraded forest to wildfires (Cochrane, 2003). In addition, other factors can exacerbate arrested succession in degraded areas. Seed banks are often poor following logging or agricultural cultivation, due to topsoil removal (Dupuy and Chazdon, 1998). Seed rain from surrounding forest into degraded land can also be limited, with wind dispersed seeds often not travelling large distances (Cubiña and Aide, 2001) and animal dispersed seeds rarely found, as few forest animals pass through such areas (Holl, 1999). Thus, the distance to the nearest primary forest can determine the success of regeneration (Cubiña and Aide, 2001). This is problematic in highly fragmented habitats where only small patches of forest remain, particularly if the species composition of such fragments is not representative of old-growth forest.

Thus, large areas of abandoned degraded land, and their propensity for arrested succession, mean that forest restoration could play a vital role in mitigating climate change. Not only could restored forest sequester carbon, they also have the potential to aid the recovery of biodiversity and ecosystem function. Collectively these factors have increased the desirability of forest restoration, often termed Forest Landscape Restoration (Chazdon et al., 2016).

Despite active management to restore forests being suggested as a potentially important method to increase terrestrial carbon storage and improve ecosystem function of tropical forests, research is sparse. In particular, very little is known about the long-term effects of forest restoration in terms of forest structure, carbon sequestration, and changes in biodiversity. This evidence is necessary as, the costs associated with forest restoration can be considerable (Lamb et al., 2005). For example, a study by Parrotta and Knowles (1999) estimated that restoration of a bauxite mine in the Amazon cost is $2500 per ha. Thus, it is important to quantify the benefits of active forest restoration to ensure restoration projects are successful enough in terms of the long-term recovery of ecosystem services to warrant the costs.

To begin to address this gap in current knowledge, we undertook research in the UWA-FACE (Uganda Wildlife Authority and FACE the future foundation) rehabilitation project, in Kibale National Park, Uganda (hereafter Kibale). Since 1995 this project has been restoring abandoned agricultural land that had become dominated by invasive elephant grass (*Pennisetum purpureum*), due to repeated wildfires (UWA-FACE, 2011). Restoration activities involved protection from fire and replanting with native tree species to restore forest ecosystem functions, and enhancing biodiversity conservation (UWA-FACE, 2007, 2011). In 2005 a study was conducted by Omeja et al. (2011a) to assess AGB and biodiversity of the project 10 years after planting.

Our aims in this study are twofold. Firstly, to quantify the effect of tree planting and fire management on AGB accumulation and plant species diversity over 18 years by remeasuring the study plots established in 2005. It is likely that the rate of AGB accumulation will change with increasing time after planting, as has been demonstrated in an Australian tropical forest restoration project (Paul et al., 2015). Specifically, we predict that initial AGB accumulation will be slow as planted seedlings have few photosynthesizing leaves, limiting growth, which will increase as the size of trees in the stand increases. Thus, we expect more recent AGB accumulation rates to be greater, and be more representative of rates over the coming decades.

Secondly, we estimate woody plant species diversity after 18 years of restoration. We expect that restoration activities will result in an increase in tree species diversity. Initially tree diversity will be dominated by planted tree species. However, the presence of planted trees is expected to assist natural regeneration and the shade created once a canopy develops will create more favourable conditions for seedlings of old-growth forest species to become established. Furthermore, the presence of planted trees will also encourage the movement of animals through the area and they will bring with them seeds of animal-dispersed species. Therefore, restoration will help increase tree diversity from pre-restoration levels, yet, it is likely to take longer for species composition to become similar to old-growth forest that forest structure of AGB due to the time delay in pioneer planted tree species being superseded by old-growth forest species.

Here, we calculate changes in forest structure, AGB and biodiversity at two periods following forest restoration, 10 years post planting in 2005 and 18 years post planting in 2013, in Kibale National Park and compare these to nearby grassland areas that have not been restored and old-growth forest that has not been degraded.

2. Methods

2.1. Study site

This study was conducted in the southern part of Kibale National Park, Uganda (E 30.31–30.36, N 0.31–0.56, Fig. 1). Kibale is a moist evergreen forest covering 795 km^2. It received on average 1672 mm y^{-1} of rainfall between 1992 and 2013 (the project duration). Rainfall distribution is bi-modal with two pronounced rainy seasons, the short rains March–May and the long rains August–November. The park elevation is 1100–1500 m.a.s.l., decreasing from north to south, which accompanies a decrease in rainfall and increase in temperature (Struhsaker, 1997).

Kibale has had some form of protection since 1932 (Baranga, 1991; Osmaston, 1959; Struhsaker, 1997), however, during the 1970s and 1980s illegal agricultural encroachment and deforestation took place in the southern part of the park (Chapman and Lambert, 2000), with ~90% of this area having undergone some form of encroachment by the 1990s (Baranga, 1991; Van Orsdol, 1986), predominantly for growing subsistence crops including banana (*Musa* sp.), cassava (*Manihot esculenta*) and maize (*Zea mays*) and the removal of timber for fuel wood (Chapman and Lambert, 2000). In 1993, the area that now forms Kibale was given national park status. An estimated 10,000–40,000 people living in the southern part of the park at this time were resettled outside the park boundary (Baranga, 1991; Chapman and Lambert, 2000; Van Orsdol, 1986).

The southern part of Kibale quickly became dominated by elephant grass (*Pennisetum purpureum*), due to repeated fires spreading from nearby subsistence farms or being set by poachers. Elephant grass can grow up to 5 m tall, severely inhibiting natural regeneration of native forest (UWA-FACE, 2011). In 1995 the UWA-FACE Natural High Forest Rehabilitation Project was initiated, a joint forest restoration project between the Uganda Wildlife Authority and FACE the future, an independent Dutch organization that aims to mitigate climate change via sustainable forest management.

The project aimed to replant of 10,000 ha of degraded habitat with native tree species, to improve biodiversity and ecological functions, whilst also producing carbon credits established via monitoring and verification of the replanted areas. By mid-2014 some 3500 ha have been replanted.

2.2. Forest restoration

Restoration consisted of protection from fire (creation and maintenance of 10 m fire breaks; staffed fire towers for monitoring) and planting areas with native seedlings (400 ha^{-1}). Seedlings were collected from surrounding forest and raised in a nursery, under partial shade, using local forest soil, without the addition

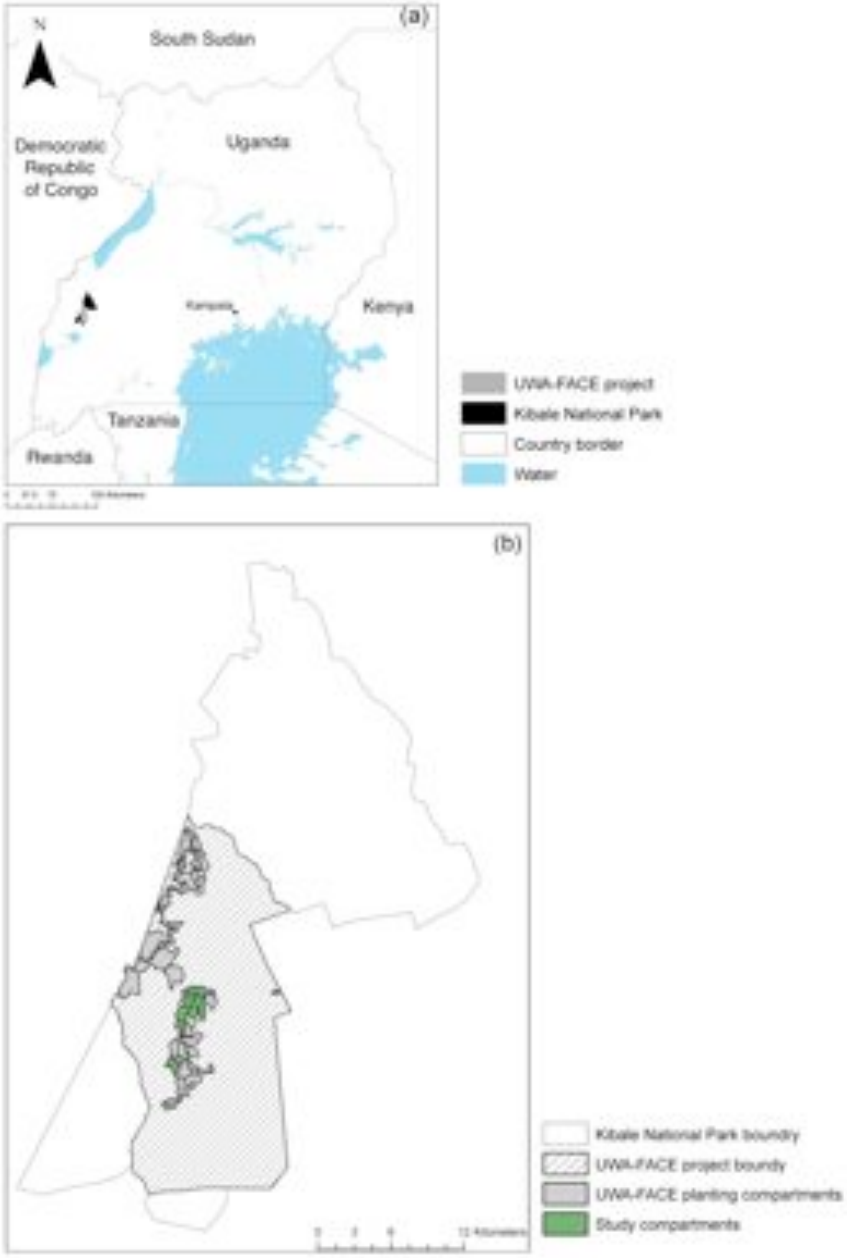

Fig. 1. Map showing location of (a) Kibale National Park within Uganda, and (b) the location of the UWA-FACE project area within Kibale and the planting compartments measured in this study.

of fertilizer (UWA-FACE, 2011). Seedlings of 0.35–1 m tall were planted every 5 m in a grid, unless an existing natural regenerating seedling occurred, when no seedling was planted. Of the 400 planting locations per ha, ~30, or 7.5%, had an existing natural regeneration, all grasses were removed surrounding these stems and therefore they were treated as planted individuals in analysis as they were given a competitive advantage over other naturally regenerating stems. Prior to planting elephant grasses were cut

at ground level in 2 m wide planting lines to reduce competition. For five years following planting, any grasses regrowing along planting lines were cut quarterly, until planted stems were >2 m tall. After five years planted areas were left unmanaged, with the exception that fires were excluded.

All areas monitored in this study were located in the Phase one area, which was the first area to be planted, between 1995 and 1997. Thirty-nine species of native tree were planted; the most common were *Markhamia platycalyx* (*Bignoniaceae*), *Uvariopsis congensis* (*Annonaceae*), *Prunus africana* (*Rosaceae*), *Lovoa brownii* (*Meliaceae*), and *Mimusops bagshawei* (*Sapotaceae*), see Appendix 1 and 2 for full list of species planted per compartment and planted species observed in 2013 within sample plots.

2.3. Plot-based study sample design

2.3.1. Sample plots

In 2005, ten years after planting, 65 plots (10 × 50 m, 3.25 ha) were established and measured by two of the researchers on the project reported here (Ometa et al., 2011a,b). Between 27th August and 8th December 2013, we remeasured 50 of these plots (2.5 ha), to assess changes over 18 years. No sampled plots underwent burning since restoration in 1995. Here we reanalyse the 2005 census data (Ometa et al., 2011a) and the new 2013 census data.

We also measured 20 plots (10 × 50 m, Total = 1 ha), across Kibale in old-growth forest to make comparisons with restoration forest. Old-growth plots were located in existing permanent sample plots (established by C. Chapman in 1989). A further six plots were established in grassland within the UWA-FACE project boundary. This area was originally forest, and underwent the same disturbance as restoration areas, however since abandonment in 1992 it has yet to receive any management. Therefore, we consider it representative of the area immediately before planting. Within this areas grassland plots were located at random but a minimum of 100 m from the grassland edge and each plot was separated by a minimum distance of 300 m.

2.3.2. Sampling within plots

Within each 0.05 ha plot area for all stems ⩾10 cm DBH (diameter at breast height) we recorded: DBH, species, height, location, and whether the stem was planted or naturally regenerating. DBH was measured at 1.3 m along the stem, except in the case of buttress roots or deformities, which were measured 50 cm above the buttress or 2 cm below the deformity respectively (Phillips et al., 2009). The height of every individual was measured using a handheld clinometer. Individuals were identified to species level were possible. In 2013, all stems >1 and <10 cm DBH were measured in three 5 × 5 m subplots (Fig. 2), recording DBH, height, and species for each individual. This data was not collected in 2005. In both 2005 and 2013 ten 1 × 1 m subplots were established through the centre of the plot at 5 m intervals for the sampling of seedlings and saplings (Fig. 2). Every seedling (i.e. <1 m tall) and sapling (1–1.99 m tall) was identified to species and the height recorded. Additionally, the percentage cover of grasses, shrubs, seedlings, and bare ground within each 1 m^2 subplot was estimated and dominant species identified. The mortality of planted stems between 1995 and 2013, was calculated (Sheil and May., 1996) as;

$$\text{Mortality } (\lambda) = \frac{\text{Ln(Stems } t_0) - \text{Ln(Stems } t_1)}{\text{Time (years)}} \quad (1)$$

where λ = instantaneous rate of change (i.e., Percentage mortality per year), t_0 = number of trees at time 0 and t_1 = number of trees at second time interval. In each of the six grassland plots three 1 m^2 samples of grasses were collected (Fig. 2), dried to constant mass and weighed to obtain the baseline above ground biomass of grasses prior to planting.

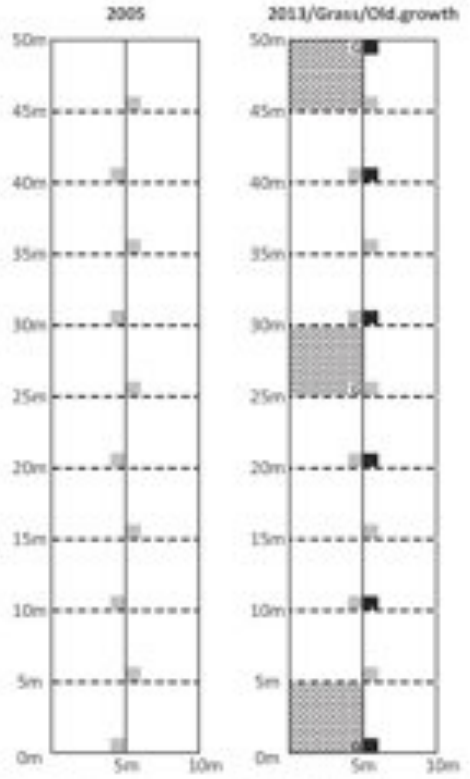

Fig. 2. Sample plot layout in restoration forest (2005, Left) and in restoration forest (2013), grassland and old-growth forest (Right). Trees ⩾10 cm DBH measured across 10 × 50 m plot, grey hashed area = trees 1 <10 m DBH measured, grey shaded area = seedlings, % ground cover measured. Black area = hemispherical photograph point, G = grass sampling point (grassland plots only).

2.3.3. Leaf area index

Hemispherical photographs were taken at 10 m intervals along the centre of the plot (n = 6, Fig. 2) to estimate leaf area index (LAI) and percentage canopy cover (8 mm F3.5 EX DG Fisheye Sigma lens; Canon 350d SLR camera; CAN-EYE V6.1 software). All six photographs from a single plot were processed together producing a mean LAI per plot, using an angular resolution of 2.5° in both Zenith (θ) and Azimuth (φ) directions. A view zenith angle of 0–60° was selected as it is a high enough resolution to extract canopy gaps of <6 cm (Leblanc et al., 2005), whilst also removing the extreme edges of the images that are dominated by woody material such as trunks so not required for LAI estimation. No hemispherical photographs were taken in 2005.

2.3.4. Data analysis

2.3.4.1. *Biomass and height.* Aboveground biomass, in Mg dry mass ha^{-1} (1 Mg = 1 metric ton) was calculated as:

$$AGB = 0.0673 \times (\rho D^2 H)^{0.976} \quad (2)$$

where ρ = wood density, D = DBH and H = height (Chave et al., 2014). Wood density values for each species were obtained from

the global wood density database (Chave et al., 2006; Zanne et al., 2009) available from the Dryad data repository (http://datadryad.org/). Where species-specific wood densities were not available, genus mean (n = 32 species) or familial mean (n = 5 species) wood densities were used (Lewis et al., 2009). If family was unknown then the mean plot wood density was used (n = 5 individuals, see Appendix 3 for full species list).

Two structural parameters were analysed: First, the asymptotic height of trees in all parameter asymptotic model of the form: $y = a(1 - \exp^{(-bx)})$, was found to be the best fit to the data for all three habitats. [Restoration forest in 2005 and 2013 and old-growth forest, Fig. S1.] Secondly, we analysed the size frequency distribution of stems using doubling size classes (1–2 cm, 2–4 cm…64–128 cm) to account for the exponential decrease in stems as DBH increases, with the expectation that old-growth forest will exhibit an inverse-J shaped distribution (Kohyama, 1986). Additionally, we assess the wood density of trees. Wood density (WD) is a readily available plant species trait that is correlated with growth and mortality and has been related to shade tolerance of tropical forest species (Philipson et al., 2014; Whitmore, 1998). In the high light environment of the restoration area, shade tolerance is likely to be an important factor in determining the survival of planted species, therefore we compare the WD of species that were planted, survived and died using ANOVA.

2.3.4.2. Biodiversity. Alpha diversity of trees (⩾10 cm DBH) and seedlings was assessed using Hill numbers, which describe biodiversity along a continuous scale from species richness to species evenness (Hill, 1973). We report Hill numbers at the extremes, N_0 = species richness and N_2 = inverse of Simpsons D index (or species evenness). Differences in α diversity were compared among habitats using analysis of variance and Tukey's HSD tests. The species composition of different habitats was compared using non-metric multidimensional scaling (NMDS), which shows dissimilarity plots and species (Lepš and Šmilauer, 2003). Biodiversity and NMDS analysis used the Vegan package (Oksanen et al., 2011) in R (R Core Team, 2013).

3. Results

3.1. Forest structure and biomass

3.1.1. Grassland

In grassland plots, which are representative of the area prior to restoration, there were no trees ⩾10 cm DBH. Total AGB was 5.1 Mg ha^{-1} (±1, 95% CI), of which 4.1 Mg ha^{-1} (80%) was elephant grass and 1 Mg ha^{-1} was saplings <10 cm DBH. Grasses dominated ground cover (66%, ±5), with some shrubs (15%, ±4) and very low seedlings cover of 1% (±0.6). Stems between 1 and 10 cm DBH had a density of 1733 (±1341), and BA of 0.8 m^2 ha^{-1} (±0.6). Canopy cover was low at 20% (±10), with an LAI of 1.4 (±0.5).

3.1.2. Replanted forest 10 years after planting

In the restoration area, ten years after planting (in 2005) the density of stems ⩾10 cm DBH had increased to 130 stems ha^{-1} (±21), with an AGB of 9.5 Mg ha^{-1} (±2.9) a basal area of 2.4 m^2 ha^{-1} (±0.5) and a wood density of 0.57 g cm^3 (±0.02). With most stems and AGB being found in the 8–16 cm size class (Fig. 3). The canopy was still relatively short with an asymptotic canopy height of 11 m (±0.6). The percentage cover of grasses had more than halved in the ten years since planting to 31% (±2), with elephant grass (*P. purpureum*) still being the most common species, found in 35% of plots. Meanwhile shrub ground cover doubled to 32% (±2) with *Lantana camara* being the most common shrub found in 36% of plots. Seedling cover increased fivefold to 5% (±1).

3.1.3. Replanted forest 18 years after planting

In the second census of the restoration plots in 2013, stem density (⩾10 cm DBH) and BA increased significantly to 349 stems ha^{-1} (±43) and 8.8 m^2 ha^{-1} (±1.4), respectively (stems p = <0.001, BA p = <0.001). AGB increased by 29 Mg ha^{-1}, to 40.6 Mg ha^{-1} (±7.7), but not significantly so (p = 0.19). There was no change in wood density (0.57 g cm^3 ± 0.01). Whilst there were more stems between 8 and 16 cm DBH, ~50% of AGB was stored in stems between 16 and 32 cm DBH (Fig. 3). Asymptotic canopy height had increased to 15 m (±1). The addition of stems between 1 and 10 cm DBH added a further 8358 stems ha^{-1} (±2880), 10 Mg ha^{-1} (±1.5) AGB and 5.4 m^2 ha^{-1} (±0.7) of BA.

The percentage cover of grasses had decreased further to 19% (±2). More importantly, the species composition of grasses changed dramatically, with an unidentified species, local name Panicum, becoming the most common species, found in 41% of plots whereas, elephant grass was found in just 4% of plots. Panicum appears not to compete so effectively with seedlings and saplings, growing to a maximum of 10 cm, and was also present in 12% of old-growth forest plots. Shrub cover increased to 44% (±3), dominated by the invasive species *L. camara*. There was no change in seedling cover. In the 18 years since planting, canopy cover increased considerably from 20% to 73% (±5), with an LAI of 4.5 (±0.3).

3.1.4. Old-growth forest

In old-growth forest stem density (⩾10 cm DBH$_1$) was not significantly greater than seen in restoration plots in 2013 (p = 0.13), at 413 stems ha^{-1} (±66). However, AGB, BA and wood density were all significantly larger than in restoration forest at 415 Mg ha^{-1} (±111, p = <0.001), 34 m^2 ha^{-1} (±5, p = <0.001), and 0.62 g cm^3 (±0.02, p = 0.003), respectively. The frequency distribution of stems is a typical inverse-J shape (Fig. 3). There is a much higher density of stems >32 cm DBH compared to restoration forest after 18 years, with 85% of AGB found in stems ⩾32 cm DBH and 55% of AGB in stems ⩾64 cm DBH (Fig. 3), and taller asymptotic canopy height at 47 m (±5). Stems between 1 and 10 cm DBH comprise 6400 ha^{-1} (±2211), 12.6 Mg ha^{-1} (±2.9) of AGB and 4.9 m^2 ha^{-1} (±0.9) of BA. The percentage cover of grasses and shrubs was not different (22% ± 3), seedling cover was higher, (12% ± 1), and canopy cover was higher, than seen in restoration forest (92% ± 2.7; LAI = 6.3 ± 0.2).

3.1.5. Biomass accumulation

Eighteen years after planting the AGB of restoration forest equates to 52% of old-growth AGB. The initial net AGB accumulation rate during the first ten years after planting of stems ⩾10 cm DBH was slow, at 0.95 Mg ha^{-1} y^{-1}. However, between 10 and 18 years after planting AGB accumulation increased to 3.9 Mg ha^{-1} y^{-1}. If AGB accumulation continued at 3.9 Mg ha^{-1} y^{-1} it would take a further 96 years for restoration forest to attain old-growth forest AGB (i.e. total 114 years).

3.1.6. Biomass accumulation and forest structure of planted versus non-planted trees

In the sample plots in 1995, an average of 390 stems ha^{-1} (±20) were planted with an additional 30 naturally regenerating stems ha^{-1} (±12) located at planting positions that received management, combined this is slightly higher than the 400 ha^{-1} expected. Planted stems had an annual mortality of 3%, leaving 153 planted stems ha^{-1} (±20) in 2013. In 2005, just 33% of AGB and 37% of BA of stems >10 cm was stored in planted stems, despite 50% of stems being planted (Table 1). By 2013, the majority of stems >10 cm were planted individuals (61%), and most AGB (69%) and BA (66%) was stored in planted stems (Table 1). Wood density of planted and non-planted stems was not significantly different in

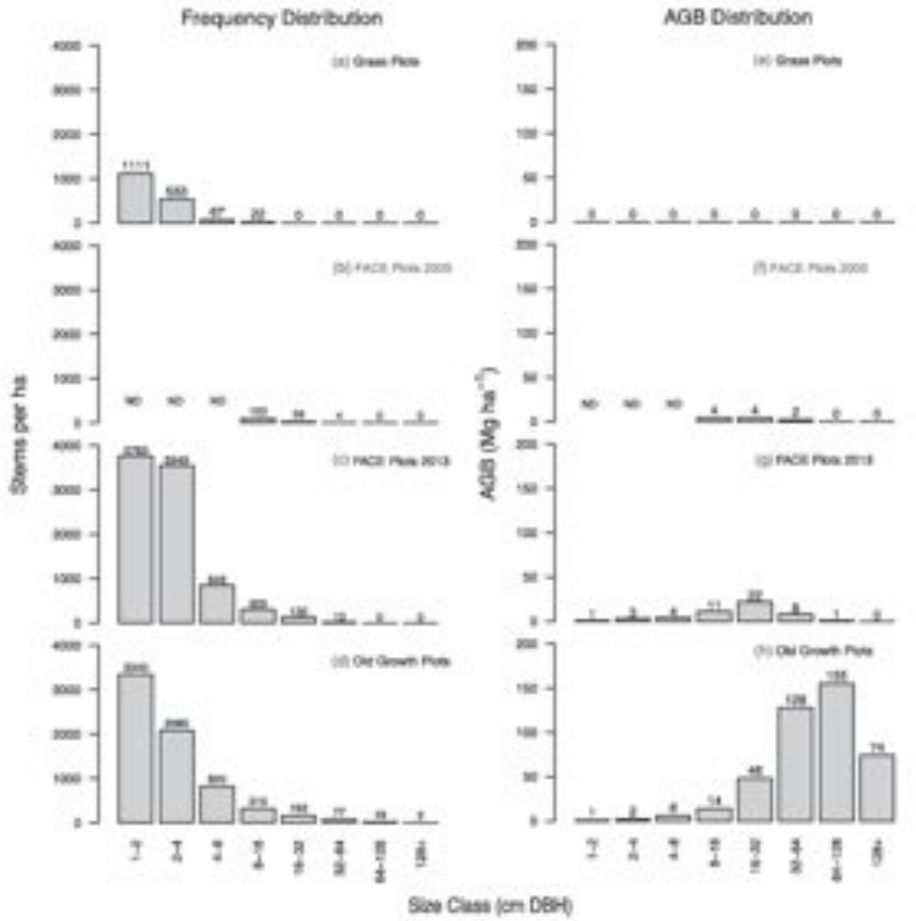

Fig. 3. Size-frequency distribution for all size classes in (a) grassland, (b) restoration plots 2005, (c) restoration plots 2013 and (d) old-growth forest plots, and above ground biomass distribution for trees ⩾ 1 cm DBH in (e) grassland, (f) FACE plots 2005, (g) FACE plots 2013 and (h) old-growth forest plots. ND = no data available (data presented for FACE plots in 2005 is only for stems ⩾ 10 cm DBH).

either census (2005: $T = -1.04$, DF = 66.2, $P = 0.3$, 2013: $T = -1.9$, DF = 95, $P = 0.07$), with planted stems having slightly high WD (Table 1). The recruitment of planted stems ⩾ 10 cm was almost double that of non-planted stems ($T = -2.6$, DF = 98, $P = 0.009$), and the AGB accumulation rate of planted stems is significantly higher than seen in non-planted stems ($T = -6.2$, DF = 71, $P = <0.0001$, Table 1). Thus, it appears that the planted stems are becoming increasingly dominant as the forest matures.

3.1.7. Biomass and structure of different planted tree species

In 1995 a total of 39 species were planted, which had a mean WD of 0.60 g cm^{-3} (±0.01). The most common species, which each constituted >10% of originally planted stems were; *U. congensis*, *Markhamia lutea*, *M. hagshawei* and *P. africana* (Table 2). These dominant planted species had a mean WD of 0.61 g cm^{-3} (±0.1). Eighteen years after planting, within the area sampled, these same four species each made up <5% of surviving planted stems (Table 2), with just two individuals of *U. congensis*, seven *M. lutea*, 12 *M. hagshawei*, and 17 *P. africana* being observed. Despite only a small proportion of the planted area being sampled, this low encounter rate of the most commonly planted species suggests they have a poor survival rate.

Ten years after planting, in 2005, seven species of planted tree ⩾ 10 cm DBH were observed, of these just three (*Bridelia micrantha*, *Warburgia ugandensis*, and *Syzium ellipticum*) made up >95% of planted stem density, AGB and BA (Table 3). Thus, the third most important 'planted' species is *S. ellipticum*, which is actually naturally regenerating with the addition of grass management. This suggests, with the exception of *B. micrantha* and *W. ugandensis* many planted species have poor survival rates. By 2013 an additional eight species of planted tree ⩾ 10 cm DBH were observed, with the same three species still dominating (Table 3). By 2013, *B. micrantha* was by far the most common planted species, making up 62% of planted stems, however it contributed just 33% of AGB (Table 3). This is due to its small size, in terms of mean DBH and height (Table 3). *W. ugandensis*, by contrast contributed 55% of planted AGB, despite making up <30% of planted stems (Table 3), as *W. ugandensis* is a much larger species than *B. micrantha*

Table 1
Total AGB, BA and stem density for planted and non-planted trees ≥ 10 cm DBH in 2005 and 2013. Accumulation rate for planted and non-planted stems between 2005 and 2013. 95% CI in parentheses.

		2005	2013	Accumulation (y^{-1})
Above ground biomass (Mg ha^{-1})	Planted	3.3 (1.1)	28.2 (5.6)	3.1 (0.7)
	Non-planted	6.6 (2.9)	12.4 (3.3)	0.7 (0.3)
Basal area (m^2 ha^{-1})	Planted	0.9 (0.2)	5.2 (0.9)	0.5 (0.1)
	Non-planted	1.5 (0.5)	3.7 (1.0)	0.3 (0.1)
Stem density (≥ 10 cm DBH ha^{-1})	Planted	62 (12)	206 (34)	18 (4)
	Non-planted	81 (15)	144 (29)	10 (3)
Wood density (g cm^3)	Planted	0.59 (0.02)	0.58 (0.02)	–
	Non-planted	0.56 (0.04)	0.58 (0.02)	–

Table 2
Mean percentage (±95% CI) of 15 most commonly planted seedlings, planted in 1995/1996 across the whole planting compartment (above line), and the percentage of total stems remaining in 2013 within the sample plot area. Species below line were observed in 2013 but were not in the top 15 most commonly planted species. ✦ = Species planted in 1995/1996 but not observed in 2013.

	1995/1996 % of all seedlings planted	2013 % of all planted trees ≥ 1 cm DBH
Markhamia platycalyx	15.1 (3.4)	1.5 (2.6)
Uvariopsis congensis	13.7 (5.2)	0.4 (0.5)
Prunus africana	11.6 (3.5)	3.3 (3.2)
Mimusops bagshawei	10.4 (5.7)	3.3 (4.0)
Lovoa brownii	8.7 (4.5)	✦
Chrysophyllum albidum	4.4 (2.4)	✦
Bilghia wildemaniana	4.4 (1.6)	0.2 (0.4)
Macaranga ugandensis	4.6 (3.8)	25 (6.4)
Strombosia schefferi	3.0 (1.4)	✦
Albizia gummifera	2.6 (2.0)	0.3 (0.5)
Bridelia micrantha	2.9 (4.4)	54.4 (14)
Diospyros mespiliformis	3.2 (2.8)	0.6 (1.2)
Antiaris toxicaria	1.7 (1.2)	✦
Spathodea campanulata	1.9 (1.1)	0.4 (0.8)
Pancovia turbinata	1.7 (0.8)	✦
Celtis durandii	1.0 (0.8)	0.2 (0.3)
Tabernaemontana holstii	0.5 (1.1)	1.9 (2.5)
Syzium ellipticum[a]		6.5 (3.8)
Croton macrostachyus[a]		1.6 (2.0)
Alkaphyllia rubiflora[a]		0.4 (0.7)

[a] Species were natural regenerating stems in 1995/1996 that received management of grasses, management of grasses.

Table 3
Mean stem density (ha^{-1}), basal area (M^2 ha^{-1}), AGB (Mg ha^{-1}) and percentage of total for planted species ≥ 10 cm DBH in 2005 and 2013. Mean DBH and height (per tree) of planted species in 2005 and 2013. 95% CI in parentheses.

		Stems (per ha)		Basal area (M^2 ha^{-1})		AGB (Mg ha^{-1})		Average DBH (cm)	Average Height (m)
		Mean	%	Mean	%	Mean	%	Mean	Mean
B. micrantha	2005	36 (12)	57.1	0.5 (0.2)	53.7	1.3 (0.8)	46.2	12.3 (0.6)	7.4 (0.6)
	2013	128 (36)	62	2.5 (0.8)	48.3	7.5 (2.7)	33.4	15.3 (0.8)	8.6 (0.6)
M. ugandensis	2005	23 (8)	36.5	0.3 (0.1)	38.1	1.3 (0.5)	44.4	13.2 (0.6)	8.4 (0.4)
	2013	55 (13)	26.7	2.2 (0.8)	41.9	12.9 (3.8)	57.8	21.7 (1.7)	12.1 (0.6)
S. ellipticum[a]	2005	2 (2)	3.2	0.04 (0.04)	4.3	0.1 (0.2)	4.6	15.8 (0.9)	9.2 (1.5)
	2013	11 (7)	5.3	0.3 (0.2)	5.6	1.2 (0.8)	5.2	18.2 (1.4)	10.4 (0.6)
Other	2005	2 (2)	3.2	0.03 (0.03)	3.9	0.1 (0.1)	4.8	14.4 (0.9)	10.3 (0.6)
	2013	12 (8)	6	0.2 (0.1)	4.4	0.8 (0.5)	3.6	22.1 (2.9)	14 (2.1)

[a] *S. ellipticum* were natural regenerating stems that received management of grasses, only species with ≥ 5 individuals sampled shown.

(Table 3). Of the naturally regenerating stems *S. ellipticum* and *B. micrantha* were the most common species making up 35% and 23% of individuals, respectively. See Appendix 4 for full list of naturally regenerating species.

Within sample plots the WD of planted species that survived until 2013 was 0.57 g cm^3 (±0.2), significantly lower than the WD of originally planted species ($T = 2.8$, $DF = 14$, $P = 0.01$). This could suggest that lower WD species, which may favour the higher light conditions found in restoration areas at the time of planting, have better survival. However the survival and growth of species is liable o change over the coming years as LAI and canopy cover increase, which would favour more shade tolerant specie.

3.2. Biodiversity and species composition

Species richness (N_0) is lowest in grassland with no trees ≥ 10 cm DBH and just two seedling species per 0.05 ha plot. As time after planting increases, so too does biodiversity, with

Table 4
Hill numbers N_0 and N_1 for grassland plots, restoration plots 2005, restoration plots 2013 and old-growth plots for trees ⩾10 cm DBH and seedlings <1 m. Plot = 0.05 ha.

	Habitat	N_0 Species richness	N_1 Inverse Simpsons D
Trees [⩾10 cm DBH]	Grass	0	0
	Restoration 2005	2.7 (0.3)	2.2 (0.2)
	Restoration 2013	4.9 (0.6)	2.9 (0.4)
	Old-growth	8.3 (1.4)	4.8 (0.9)
Seedlings [<1 m]	Grass	1.7 (1.1)	1.6 (1.0)
	Restoration 2005	2.5 (0.9)	1.1 (0.2)
	Restoration 2013	8.5 (0.7)	3.7 (0.5)
	Old-growth	15.8 (2.6)	5.8 (1.3)

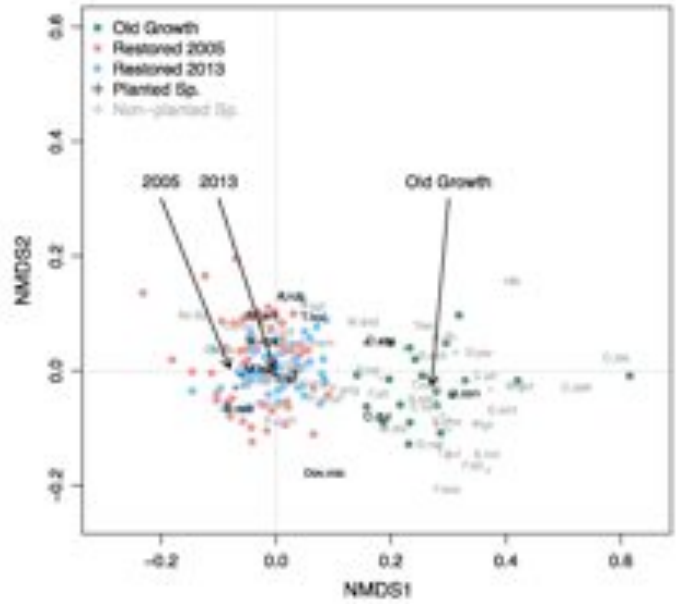

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination plot showing community composition of trees ⩾10 cm DBH. Species names in black were planted and species names in grey were naturally regenerating (non-planted). Arrows indicate mean NMDS scores for each habitat. Species codes are first letter of genus and first three letters of species name. Species shown: *Acacia* spp., *Albizia grandibracteata*, *Albizia gummifera*, *Alkophyllus nobilobus*, *Aningeria altissima*, *Antidesma membranaceum*, *Begbiegia parviflora*, *Beguaertiodendron natalense*, *Bosqueia phoberos*, *Bridelia micrantha*, *Celtis africana*, *Celtis durandii*, *Celtis zenkeri*, *Combretum molle*, *Cradisa* spp., *Croton macrostachyus*, *Cynometra alexandri*, *Dovyalis microcarpa*, *Ehretia cymosa*, *Euadenia eminens*, *Ficus capensis*, *Ficus exasperata*, *Funtumia africana*, *Funtumia latifolia*, *Gardenia lanciloba*, *Harrisonia abyssinica*, *Kigelia moosa*, *Mangifera indica*, *Markhamia lutea*, *Markhamia platycalyx*, *Minusops bagshawei*, *Mimbrenera aindura*, *Mitrandra guineensis*, *Newtonia buchananii*, *Pipadeniastrum*, *Pleiocarpa pycnantha*, *Premna angolensis*, *Rauvolfia vomitoria*, *Sapium ellipticum*, *Sparkedea campanulata*, *Strombosia schafferi*, *Strychnos mitis*, *Tabernaemontana holstii*, *Teclea nobilis*, *Trichilia dregeana*, *Uvariopsis congensis*, *Vangueria apiculata*, *Warburgia ugandensis*.

restoration plots in 2013 having two more tree species and six more seedling species per plot than restoration plots in 2005 (Table 4). Nevertheless, by 2013, restoration plots still have significantly fewer tree species ($t = 4.3$, DF = 26, $P = 0.0002$) and seedling species ($t = 5.4$, DF = 22, $P < 0.0001$), than old-growth forest, which has 8 tree and 16 seedling species per plot (Table 4).

Species evenness (N_1) in stems ⩾10 cm also increases in restoration plots between 2005 and 2013, but by very little, suggesting that 18 years after planting, a small number of species still dominate (Table 4). Seedling species evenness increases more than that of trees in restoration plots between 2005 and 2013 (Table 4). However, species evenness in restoration plots in 2013 is still significantly lower than in old-growth forest for both trees ($t = 3.6$, DF = 27, $P = 0.001$) and seedlings ($t = 3.6$, DF = 26, $P = 0.001$).

NMDS plots showed that the community composition of trees ⩾10 cm DBH in restoration forest and old-growth forest differ markedly. There was a clear clustering of sample plots along NMDS axis 1, with restoration forest plots in 2005 and 2013 noticeably overlapping to the left of axis 1 and old-growth forest plots clustered to the right (Fig. 4). The mean NMDS scores in restoration forest in 2013 had shifted to the right along NMDS axis 1, which suggests that species composition was becoming more similar to old-growth forest. There was also some clustering of planted species (in black) over restoration forest plots on the left of NMDS axis 1 (Fig. 4). There were some planted species that did not overlap with restoration forest plots, notably *U. congensis* (U.con in Fig. 4), this is a species that was rarely encountered in restoration forest despite being planted, but was common in old-growth forest.

4. Discussion

4.1. Effects of active restoration on above ground biomass and carbon sequestration

This study demonstrates that the effective restoration of this heavily degraded tropical forest site is possible using a combination of management to exclude fire plus tree planting. Above ground biomass accumulation of stems ⩾10 cm DBH increased fourfold to 3.9 Mg ha $^{-1}$ y $^{-1}$ between 10 and 18 years, showing significant carbon sequestration. This result shows a danger of relying on short-term studies to predict long-term accumulation of AGB in restoration forest, as early AGB accumulation rates are likely to be unrepresentative of long-term trends. Indeed, using the first 10 year accumulation rate suggests it would take a further 400 years for AGB to reach old-growth levels, whereas we estimate if will take a further 96 years. The initially slow rate of AGB accumulation is likely due to two factors. Firstly, the relatively small numbers of photosynthesizing leaves on small tree seedlings means that growth is slow. Secondly, as dense elephant grass (*P. purpureum*) was removed (~5 Mg ha $^{-1}$), new growth from seedlings must compensate for this before there is a net AGB increase.

After 18 years restoration forest is still in the early stages of succession therefore it is uncertain how the rate of AGB accumulation will change in the future. However, we could predict that the maximum rate of AGB accumulation would not exceed the rate of above-ground wood production (AGWP) seen in nearby old-growth forest permanent sample plots, of 6.9 Mg dry mass ha $^{-1}$ y $^{-1}$ (±1.2, 95% CI, C. Chapman, unpublished data). AGWP is calculated as the difference in AGB for stems that were present in the first and second census, plus the AGB of any new stems that appeared in the second census (Talbot et al., 2014), i.e. the new additions of woody dry mass into the forest system. Accumulation of AGB is equal to AGWP *minus* biomass losses due to mortality, therefore maximum AGB accumulation is likely to be lower than AGWP. However, AGWP is still considerably higher than the AGB accumulation rate calculated in this study, suggesting that increases in carbon sequestration in the restoration plots are possible.

Once the restoration forest canopy fully closes the stand will likely start to self-thin, with slower growing, shade tolerant late-successional species beginning to supersede the planted pioneer trees and early successional species (Finegan, 1996; Rees et al., 2001). This will create a more uneven aged stand, mimicking the recruitment and mortality dynamics seen in old-growth forest (Sheil and May, 1996). An increase in mortality will eventually lead to a reduction in overall AGB accumulation rate, at the stand level, as the stand approaches the AGB of old-growth forest (Lichstein et al., 2009).

We know of only three studies that monitored active tropical forest restoration for a period greater than 18 years, all from Australia (Cairnsell et al., 2012; Kanowski et al., 2003; Preece et al., 2012). However, all of these studies were forest chronosequence studies, rather than repeated measurements of permanent sample plots, and only one estimated AGB accumulation (Preece et al., 2012). Therefore, we believe our study is the longest duration study of tropical restoration using repeated sampling. Preece et al. (2012) estimated AGB accumulation of 12 Mg ha $^{-1}$ y $^{-1}$ in restored forest, much higher than our 3.9 Mg ha $^{-1}$ y $^{-1}$ estimate. Whilst AGB accumulation rates of over 12 Mg ha $^{-1}$ y $^{-1}$ have been recorded in the tropics (e.g. Fehse et al., 2002; Hertel et al., 2009), these have generally be located in habitats different to that found in Kibale. For example Fehse et al. (2002) estimated AGB accumulation of 14.2 Mg ha $^{-1}$ y $^{-1}$ during the first 8 years following logging, however, this was in high altitude (>3000 m) forest in Ecuador. The high AGB accumulation rate estimated by Preece et al. could be a result of AGB accumulation being averaged across three different planting types, which included eucalyptus plantations, mixed timber plantations, and diverse 'ecological' plantations. The inclusion of fast growing eucalyptus plantations may have resulted in a higher accumulation rate that is not representative of biomass accumulation in ecological restoration projects if measured alone.

A recent pair of studies (Martin et al., 2013; Poorter et al., 2016) predicted the time it would take for the AGB of abandoned agricultural land to reach that seen in old-growth. In a meta-analysis of 74 studies Martin et al. (2013), found that tropical secondary forest, with no management interventions, reached old-growth forest AGB in an average of 80 years. Meanwhile, in an analysis of 45 neotropical sites, Poorter et al. (2016) predicted it would take 66 years for abandoned agricultural land to attain 90% of old-growth forest AGB. In both cases this is shorter than the further 96 years predicted in this study for restoration forest to reach old-growth forest AGB. There are a number of possible explanations for this difference. Firstly, the majority of studies used by Martin et al. (2013) and all of the site in Poorter et al. (2016) were from Latin America and therefore may have different climatic conditions to Kibale. Secondly, in Martin et al. their definition of secondary forest was 'previously forested land undergoing secondary succession following total or near total removal of trees'. Therefore, some areas may have started with higher initial AGB than the low 5 Mg ha $^{-1}$ at Kibale. Thirdly, Poorter et al. excluded sites that were experiencing arrested succession, as was the case in Kibale, and state that this could lead to slight overestimation of recovery rates. Finally, the AGB of old-growth forest may be lower than the 415 Mg ha $^{-1}$ seen in Kibale, as AGB is lower over large areas of Latin America compared to Africa, meaning old-growth levels are attained more quickly (c.f. Amazon and Africa AGB, Baker et al., 2004; Lewis et al., 2013).

In the 18 years since planting, the 1305 ha in the Phase one planting area (where all restoration plots are located) have sequestered an estimated 24,920 Mg of carbon (lower and upper confidence interval = 20,198–29,643 Mg of carbon. Carbon = 47.1% [±0.4] of AGB, Thomas and Martin, 2012). In subsequent planting phases an additional 1936 ha have been planted (3241 ha planted in total to date). Using the accumulation rates calculated in this study an estimated 47,770 Mg of Carbon has been sequestered by the UWA-FACE project by 2013. If the entire 10,000 ha project area were planted and fully restored to reach old-growth forest levels of aboveground carbon storage, the UWA-FACE project area would sequester ~2 Tg carbon (range 1.5–2.5 Tg C, 1 Teragram = 10^{12} = 1 million Mg). Indeed, 2 Tg C is a minimum estimate as it excludes belowground and necromass carbon pools. In old-growth forest carbon storage in belowground and necromass pools are ~25% and ~13% of aboveground carbon, respectively (Delaney et al., 1998; Lewis et al., 2009; Phillips et al., 2008), which would contribute an additional ~0.8 Tg C. This is a first-order estimate, as aboveground to belowground and necromass ratios may differ with forest age and structure. Preece et al. (2015) found an aboveground to belowground ratio of 24% in young ecological restoration forest, planted on abandoned pasture, suggesting that this is a reasonable estimate for belowground carbon stocks in the UWA-FACE project. Over the whole project there is a very large potential store of carbon showing the benefits of active forest restoration in an area of degraded forest affected by arrested succession.

All project activities, which include: preparation of land for planting (~10 person days ha $^{-1}$); planting seedlings (~7 person days ha $^{-1}$); management of grasses surrounding planted seedlings (~3 person days ha $^{-1}$); and maintenance of firebreaks cost ~$1200 per ha over 5 years (UWA-FACE, 2011). If all 10,000 ha of the project area were fully restored the full project costs would

be $12 million. Assuming that the entire project area were accumulating carbon at a rate of 1.85 Mg ha^{-1} y^{-1} (i.e. 3.9 Mg ha^{-1} y^{-1} of dry biomass with a carbon content of 47.1% or 18,500 Mg y^{-1} across the whole project area), for the project to break-even within 20 years, carbon would need to be priced at $32 per tonne (i.e. $12 million/20 years = $600,000 per year to sequester 18,500 Mg C y^{-1} = $32 per tonne). Including belowground carbon and longer projects, of course, both lower carbon prices. This shows that allocating a relatively high carbon prices are necessary if funding for restoration projects such as this is to become readily available.

4.2. Effects of active restoration on biodiversity

These study results also suggest that forest restoration is beneficial for plant biodiversity, with both trees ⩾10 cm DBH and seedlings <2 m increasing in species richness and evenness since planting (Table 4). However, biodiversity of trees and seedlings is still significantly lower than old-growth forest (Table 4). Furthermore, restoration and old-growth plot had markedly difference species composition (Fig. 4). These results support the hypothesis that forest restoration will improve biodiversity, but species composition will take longer to reach old-growth forest levels than AGB, as early successional pioneers tree species, which make up the majority of planted stems are relatively rarely found in old-growth forest. Species composition will become more similar to that of old-growth forest only after the planted pioneer species are superseded, which usually takes a few decades – the average lifespan of many pioneer species (Rees et al., 2001). This is in accordance with a meta-analysis by Martin et al. (2013) who found that in secondary forest, AGB recovery was more rapid than biodiversity recovery. They estimated that tree diversity would reach old-growth forest levels within 100 years, 20 years longer than for ABG to reach old-growth forest levels. They suggested this was a result of the sensitivity of old-growth forest specialists to human disturbance, coupled with small ranges and populations of old-growth species. However, while forest restoration has often been suggested as an important possible approach to slowing biodiversity losses (Bekessy and Wintle, 2008), and changes in biodiversity have been well documented in natural regenerating forest (Barlow et al., 2007; Martin et al., 2013), to our knowledge ours if the first study into the effect of active restoration on plant biodiversity. Our study highlights the co-benefits that forest restoration may secure for plant biodiversity and carbon sequestration.

4.3. Necessity of active restoration

Without restoration activities it is likely that natural regeneration in Kibale would be extremely limited. This is evident in grassland plots that were not protected from fire and remain dominated by the grass *P. purpureum* 22 years after farming was abandoned, where AGB is 5.1 Mg ha^{-1}. These grassland areas have undergone a burning regime since abandonment in 1992, similar to that which replanted areas experienced prior to the building of fire-breaks and planting. The occasional trees present in grassland were generally fire resistant species, such as *Erythrina abyssinica*, *Combretum molle*, and *Acacia* spp.

Besides managing fire, the planting of seedlings is important for the restoration of heavily degraded land, as after 18 years, almost 70% of AGB is stored in planted trees. Furthermore, planted stems have a much higher AGB accumulation rate than non-planted stems, at 3.1 Mg ha^{-1} y^{-1} verses 0.7 Mg ha^{-1} y^{-1} (Table 1). It is likely that this higher rate of accumulation results from planted stems being given a competitive advantage over non-planted stems due to the regular removal of surrounding grasses early in the restoration process. This assumption is supported by the growth seen in naturally regenerating seedlings that underwent the same management (cutting of grasses) as planted seedlings. These included *S. ellipticum*, which were not planted, but treated in the same way, when they occurred at planting points, which by 2013 was the third most common tree in the planted stands. This suggests that the tending of seedlings, notably reducing competition with grasses, is an important management intervention. Of course, adopting tending of naturally regenerating seedlings as a management technique is dependent on the abundance of naturally regenerating seedlings in grassland areas, which in this study was only ~30 individuals per ha. Cost may become important, as planting in lines to a standard plan gives easier management and possible economies of scale. However, our findings suggest that management to assist the competitive release of naturally regenerating seedlings deserves further study.

Although it is clear that restoration in this heavily degraded region is essential for recovery of AGB and biodiversity, it is unclear whether the combination of fire protection and replanting is necessary for successful restoration or whether fire protection alone would be a suitable restoration technique. A study by Omeja et al. (2011b) estimated AGB in a 0.5 ha grassland plot that was protected from fire for 32 years, also located within Kibale. They found that after 32 years of natural regeneration, AGB of stems ⩾10 cm DBH was 29.9 Mg ha^{-1}, accumulating at a rate of 0.9 Mg ha^{-1} y^{-1}. They also observed species richness, of trees ⩾10 cm DBH, of 24 species per 0.5 ha plot. This result suggests that natural regeneration of AGB and biodiversity is possible if areas are just protected from fire. However, AGB accumulation in this fire-only protected area is slower than measured in the UWA-FACE project, with an AGB of 40.6 Mg ha^{-1} after 18 years. If AGB were to continue accumulating at the estimated rate of 3.9 Mg ha^{-1} y^{-1}, after 32 years the AGB in restoration forest could potentially reach 95.2 Mg ha^{-1}, more than triple that seen in areas just protected from fire. While Omeja et al. (2011b) only studied a single 0.5 ha fire protected plot, it suggests that the combination of fire protection, planting, and the regular removal of nearby competitors of these seedlings, accelerate carbon sequestration and biodiversity increases compared to fire protection alone.

4.4. Problems with active restoration

After 18 years, only 15 of the 39 species that were originally planted were observed in the 50 sample plots. *B. microntha* and *W. ugandensis*, were the dominant species in 2013, but made up <5% of originally planted stems. Both are pioneer species rarely seen in old-growth forest (Katende et al., 1995; UWA-FACE, 2011). Conversely, *M. platycalyx*, *U. congensis*, *P. africana*, and *M. bagshawei* each constituted >10% of originally planted stems (Table 3), but were rarely encountered in 2013, making up between 0.4% and 3% of planted stems (Table 3). The low encounter rate of commonly planted species demonstrates the importance of selecting species with high seedling survival. Pilot studies to evaluate which survival will be extremely useful in improving future restoration, as noted previously in the literature (e.g. Brancalion et al. (2011) in a Brazilian context).

The UWA-FACE project adopted a more-or-less trial and error approach. Early planting regimes were monitored to improve the next round of species selection and planting. In the Phase 1 planting area, where this study was carried out, 39 different species were planted, reduced to 22 in Phase 2 and 3 (1997–2002), 16 in Phase 4 and 5 (2003–2006), and 10 species in Phase 6 (2007 onwards). These 10 species with low mortality and high growth rates are; *B. microntha* (*Euphorbiaceae*), *Cordia africana* (*Boraginaceae*), *Cordia millenii* (*Boraginaceae*), *Croton macrostachys* (*Euphorbiaceae*), *Croton megalocarpus* (*Euphorbiaceae*), *Ficus natalensis* (*Moraceae*), *M. bagshawei*, *P. africana*, *Sparhodea campanulata*

(Bignoniaceae) and *W. ugandensis* (Canellaceae) (UWA-FACE, 2011). This has led to some Phase 2 and 3 areas resembling the 18 year old restoration forest in Phase 1 after only 11–16 years (lead author, personal observation).

Possibly the biggest ecological problem that could influence the continuation of the forest restoration, is the invasion of the dense shrub *L. camara*, which is the most common shrub in plots in both 2005 and 2013. Native to South America, *L. camara* is planted in nearby villages as an ornamental shrub. It is an extremely fast growing shrub that forms dense thickets, shading out the forest floor and inhibiting the regeneration of seedlings (Zalucki et al., 2007). Across most of its invasive range the spread of *L. camara* is not considered to be under sufficient control (Zalucki et al., 2007). Management of *L. camara* may be required in the future, which may include: slashing of plants at base, burning, uprooting, chemical control with herbicides and biological control using natural predators (Love et al., 2009).

5. Conclusion

This study adds to the very limited active forest restoration literature. Just three studies were found that monitored restored forest over 18 years, as has been done in this study. However, these used forest chronosequences, thus no previous studies measure changes in AGB over a long time period, using repeat censuses of permanent sample plots, as this study does, the most reliable sampling method.

It is clear that protection from fire, planting seedlings, and grass cutting, is a successful restoration method, leading to the recovery of above ground biomass, forest structure and biodiversity. Indeed, active restoration of this site is essential for the recovery of this highly degraded area as ~70% of AGB is stored in planted stems after 18 years. However, restoration is a slow process with ~100 years required for restoration forest to reach old-growth forest levels of AGB. For species composition, the delay is likely to be much longer. Therefore, the continued protection of this area is essential if restoration forest is to reach old-growth forest levels of biodiversity and carbon storage.

The continued monitoring of permanent sample plots into the future is needed to understand the long-term dynamics of recovery in restoration forest. The large increase in AGB accumulation from 0.95 Mg ha^{-1} y^{-1} between 0 and 10 years to 3.9 Mg ha^{-1} y^{-1} between 10 and 18 years demonstrates that short-term studies are not accurate in determining long-term trends in restoration forest. The sizeable carbon sequestration benefits possible, ~2 Tg C if all 10,000 ha were restored and attained old-growth AGB level, from this project supports the idea of ecologically friendly tropical forest restoration under schemes such as REDD+, whilst also offering the co-benefit of biodiversity conservation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.04.025.

References

Baker, T.R., Phillips, O.L., Malhi, Y., et al., 2004. Increasing biomass in Amazonian forest plots. Philos. Trans. R. Soc. Lond. Set. B – Biol. Sci. 359, 353–365.

Barongo, J., 1993. Kibale Forest Game Corridor: Man or Wildlife? Surrey Beatty & Sons, Australia.

Barlow, J., Gardner, T.A., Araujo, I.S., et al., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. USA 104, 18555–18560.

Bekessy, S.A., Wintle, B.A., 2008. Using carbon investment to grow the biodiversity bank. Conserv. Biol. 22, 510–513.

Bongers, M.V., Hall, J.S., Craven, D.J., et al., 2011. Early growth and survival of 40 tropical tree species across sites differing in soil fertility and rainfall in Panama. For. Ecol. Manage. 261, 1580–1589.

Cantrell, C.P., Freeman, A.N., Karsenski, J., Fourbody, K., 2012. Can active restoration of tropical rainforest rescue biodiversity? A case with bird community indicators. Biol. Conserv. 146, 53–61.

Chapman, C.A., Lambert, J.E., 2000. Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. Am. J. Primatol. 50, 169–185.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Ter Steege, H., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecol. Appl. 16, 2356–2367.

Chave, J., Réjou-Méchain, M., Búrquez, A., et al., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biol. 20, 3177–3190.

Chazdon, R.L., Brancalion, P.H.S., Laestadius, L., et al., 2016. Where is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. Ambio, 1–13.

Cochrane, M.A., 2003. Fire science for rainforests. Nature 421, 913–919.

Cubiña, A., Aide, T.M., 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. Biotropica 33, 260–267.

Deans, J.D., Moran, J., Grace, J., 1996. Biomass relationships for tree species in regenerating semi-deciduous tropical moist forest in Cameroon. For. Ecol. Manage. 88, 215–225.

Dupuy, J.M., Chazdon, R.L., 1998. Long-term effects of forest regrowth and selective logging on the seed bank of tropical forests in NE Costa Rica. Biotropica 30, 223–237.

Ferbe, J., Hofstede, R., Aguirre, N., Paladines, C., Ronquim, A., Sevink, J., 2002. High altitude tropical secondary forests: a competitive carbon sink? For. Ecol. Manage. 163, 9–25.

Finegan, B., 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. Trends Ecol. Evol. 11, 119–124.

Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., Leuschner, C., 2009. Below- and above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi, Indonesia) as compared to neotropical forests. For. Ecol. Manage. 258, 1904–1912.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432.

Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.

Kanowski, J., Catterall, C., Wardell-Johnson, G., Proctor, H., Reis, T., 2003. Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. For. Ecol. Manage. 183, 265–280.

Katende, A.B., Birnie, A., Tengnas, B., 1995. Useful trees and shrubs for Uganda. Identification, propagation and management for agricultural and pastoral communities. Regional Soil Conservation Unit, Nairobi, 9966, 22.

Kohyama, T., 1980. Tree size structure of stands and each species in primary warm-temperate rain forests of southern Japan. The Botanical Magazine = Shokubutsu-gaku-zasshi 93, 267–278.

Lamb, D., Erskine, P., Parrotta, J., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–1632.

Lawes, M., Chapman, C., 2006. Does the herb *Acanthus pubescens* and/or elephants suppress tree regeneration in disturbed Afrotropical forest? For. Ecol. Manage. 221, 278–284.

Leblanc, S.G., Chen, J.M., Fernandes, R., Deering, D.W., Conley, A., 2005. Methodology comparison for canopy structure parameters extraction from digital hemispherical photography in boreal forests. Agric. For. Meteorol. 129, 187–207.

Legd, JÉ, Šmilauer, Petr, 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, New York.
Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., et al., 2009. Increasing carbon storage in intact African tropical forests. Nature 457, 1003–1006.
Lewis, S.L., Sonké, B., Sunderland, T., et al., 2013. Above-ground biomass and structure of 260 African tropical forests. Philos. Trans. R. Soc. B: Biol. Sci. 368.
Lichstein, J.W., Wirth, C., Horn, H.S., Pacala, S.W., 2009. Biomass consequences of United States forests: implications for carbon storage and forest management. In: Old-Growth Forests. Springer, pp. 301–341.
Love, A., Babu, S., Babu, C.R., 2009. Management of Lantana, an invasive alien weed, in forest ecosystems of India. Curr. Sci. 97, 1421–1429.
Martin, P.A., Newton, A.C., Bullock, J.M., 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proc. R. Soc. B – Biol. Sci. 280.
Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H, Wagner, H., 2013. Vegan: Community Ecology Package. <http://CRAN.R-project.org/package=vegan>.
Ostreja, P., Chapman, C., Obua, J., Lwanga, J., Jacob, A.L., Wanyama, F., Mugenyi, R., 2011a. Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation in Kibale National Park, Uganda. For. Ecol. Manage. 261, 703–709.
Ostreja, P., Lwanga, J., Obua, J., Chapman, C., 2011b. Fire control as a simple means of promoting tropical forest restoration. Trop. Conserv. Sci. 4, 287–299.
Osmaston, H.A., 1950. Forestry Working Plan for the Kibale and Kwaca Forests. Uganda Forest Department, Entebbe, Uganda.
Pan, Y., Birdsey, R.A., Fang, J., et al., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993.
Parrotta, J.A., Knowles, O.H., 1999. Restoration of tropical moist forests on Bauxite-Mined lands in the Brazilian Amazon. Restor. Ecol. 7, 103–116.
Paul, J.R., Randle, A.M., Chapman, C.A., Chapman, L.J., 2004. Arrested succession in logging gaps: is tree seedling growth and survival limiting? Afr. J. Ecol. 42, 245–251.
Paul, K.I., Roxburgh, S.H., England, J.R., et al., 2015. Improved models for estimating temporal changes in carbon sequestration in above-ground biomass of mixed-species environmental plantings. For. Ecol. Manage. 338, 208–218.
Philipson, C.D., Dent, D.H., O'Brien, M.J., et al., 2014. A trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific relative growth rates. Ecol. Evol. 4, 3675–3688.
Phillips, O., Baker, T., Feldpausch, T., Brienen, R., 2009. RAINFOR Field Manual for Plot Establishment and Remeasurement. <http://www.rainfor.org/en/manuals>.
Phillips, O.L., Lewis, S.L., Baker, T.R., Chao, K.J., Higuchi, N., 2008. The changing Amazon forest. Philos. Trans. R. Soc. B – Biol. Sci. 363, 1819–1827.
Poorter, L., Bongers, F., Aide, T.M., et al., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214.
Pearce, N.D., Crowley, G.M., Lawes, M.J., Van Oosterzee, P., 2012. Comparing above-ground biomass among forest types in the Wet Tropics: small stems and plantation types matter in carbon accounting. For. Ecol. Manage. 264, 228–237.
Pearce, N.D., Lawes, M.J., Bowman, A.K., Curran, T.J., Van Oosterzee, P., 2015. Modelling the growth of young rainforest trees for biomass estimates and carbon sequestration accounting. For. Ecol. Manage. 354, 57–66.
R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
Rees, M., Condit, R., Crawley, M., Pacala, S., Tilman, D., 2001. Long-term studies of vegetation dynamics. Science 293, 650–655.
Sholl, D., May, R.M., 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. J. Ecol. 84, 91–100.
Struhsaker, T.T., 1997. Ecology of an African Rainforest: Logging in Kibale and the Conflict between Conservation and Exploitation. University Press of Florida, Gainsville, Florida.
Talbot, J., Lewis, S.L., Lopez-Gonzalez, G., et al., 2014. Methods to estimate aboveground wood productivity from long-term forest inventory plots. For. Ecol. Manage. 320, 30–38.
Thomas, S.C., Martin, A.R., 2012. Carbon content of tree tissues: a synthesis. Forests 3, 332–352.
Uwa-Face, 2007. Natural high forest rehabilitation project on degraded land of Kibale National Park. In: Verified Carbon Standard Project Description Template.
Uwa-Face, 2011. UWA-FACE the Future Annual Plan of Operations. Uganda Wildlife Authority, Fort Portal, Uganda.
Van Orsdol, K.G., 1986. Agricultural encroachment in Uganda's Kibale Forest. Oryx 20, 115–117.
Whitmore, T.C., 1998. An Introduction to Tropical Rain Forests. Oxford University Press, Oxford.
Zahacki, M., Day, M., Playford, J., 2007. Will biological control of Lantana camara ever succeed? Patterns, processes & prospects. Biol. Control 42, 251–261.
Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R. B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Global Wood Density Database, Dryad. <http://hdl.handle.net/10255/dryad.235>.